

# FEEDING SELECTIVITY OF SCHOOLS OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, IN THE SOUTHERN CALIFORNIA BIGHT

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## ABSTRACT

Direct field measurements of the feeding of five schools of northern anchovy over four sets of conditions indicate consistent size-selective feeding on the dominant zooplankton taxa. At low-to-moderate prey concentrations (10-40 mg carbon per cubic meter), the schools consumed 35-50% of the total zooplankton biomass and >90% of the largest zooplankters present. The schools' feeding was a positive function of prey size primarily. The density of particular prey items did not significantly affect feeding selectivity. The northern anchovy fed preferentially upon a particular species in only one instance. No significant difference was found in the selectivity of two northern anchovy schools composed primarily of late 0-group and II-group fish, respectively, that were feeding under similar feeding conditions. At prey concentrations of 10-40 mg carbon per cubic meter, the degree of selectivity was inversely related to the size of the largest prey available. The prey size at which consumption is predicted to be 100% was proportional to the size of the largest prey.

Field studies have demonstrated that planktivorous fish can control zooplankton community structure in oligotrophic lakes and stocked fish ponds by selectively feeding upon the larger, more visible prey organisms (see Gliwicz and Prejs 1977 and Dodson 1979 for a critical discussion of this work). However, while highly productive regions in the world's oceans typically support large populations of schooling, planktivorous fish, the impact of these fish populations upon marine zooplankton communities is not known.

Taking as an example the estimated consumption of zooplankton by the northern anchovy, *Engraulis mordax*, in the Southern California Bight, it becomes clear that marine fish populations may have considerable impact on the zooplankton in the system. The prey consumption of the northern anchovy may be calculated based upon data for the biomass of the population, its annual reproduction and growth, and assumptions concerning its metabolic efficiency. The results of this calculation can then be compared with estimates of zooplankton production in the region.

In the Southern California Bight, the spawning biomass of the northern anchovy in the mid-1960's to early 1970's averaged between 1.32 and  $2.35 \times 10^6$  t over a  $40 \times 10^3$  km<sup>2</sup> area or 1.34-2.25

g C/m<sup>2</sup> (calculated from Smith 1972). *Engraulis mordax* spawns approximately 20 times annually and produces 389 eggs/g wet weight at each spawning (Hunter and Goldberg 1980). Averaged over the year, this is equivalent to a daily production rate of 0.43%, based upon a dry weight per egg of 0.030 mg (Hunter and Leong<sup>2</sup>) or 0.20 mg wet weight (assuming a 15% wet weight:dry weight conversion):  $[(389 \times 20 \times 0.2 \times 10^{-3}) / 365] \times 100 = 0.43$ .

The growth rate of the northern anchovy past the first year of life is negligible, approximately 0.08%/d from the end of the first year to the end of the third year (calculated from Sakagawa and Kimura 1976). The total daily production of the adult northern anchovy is thus approximately 0.43% + 0.08% = 0.51%. Assuming a 10-30% efficiency of food conversion (Paloheimo and Dickie 1966 and references therein; Jones and Hislop 1978; Lane et al. 1979), mature northern anchovy consume 1.7-5.1% of body weight daily:  $0.51 \times 1/0.30 = 1.7$ ;  $0.51 \times 1/0.10 = 5.1$ . [The food consumption rate for 0-group northern anchovy is considerably greater since the daily growth rate during the first year is about 6.1% (calculated from Sakagawa and Kimura 1976).] The mature northern anchovy stock therefore consumes

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<sup>2</sup>Hunter, J. R., and R. Leong. The spawning energetics of female northern anchovy, *Engraulis mordax*. Unpubl. manuscript. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

0.02-0.11 g C/m<sup>2</sup> per d. Primary production in the Bight averages 0.5-1.0 g C/m<sup>2</sup> per d (Eppley et al. 1979). The northern anchovy feeds primarily upon zooplankton. Assuming a 20% conversion of primary to secondary production, the spawning population of *E. mordax* consumes 10 to >100% of secondary production in the Southern California Bight. This figure appears to give the right order of magnitude, since >80% of acoustic targets from pelagic surveys in this area are estimated to be northern anchovy schools (Mais 1974). It should be noted that the Southern California Bight appears to be an area of net zooplankton consumption, since zooplankton densities are typically greater in the California Current north of the Bight than in the Bight itself (Reid 1962). Presumably the zooplankton are being consumed as they are carried into the area. The northern anchovy also supplements its diet by filter feeding on phytoplankton.

If the feeding of the northern anchovy is size selective, its impact on the community of zooplankton could be considerable. Furthermore, the northern anchovy population is, relatively speaking, not all that large. The population of the Peruvian anchovetta, which is predominantly phytophagous but is a zooplankton feeder in certain areas and at certain stages of its life history (Rojas de Mendiola 1971), is estimated to have been an order of magnitude more densely concentrated (Walsh et al. 1980).

Most quantitative studies of the feeding selectivity of marine fish have been conducted in the laboratory with small groups of fish (Leong and O'Connell 1969; O'Connell 1972; Durbin and Durbin 1975). This permits only a crude approximation of their impact upon marine systems, where these fish populations are predominantly found in massive shoals. For example, approximately 90% of the biomass of the northern anchovy population is found in schools >25 t (calculated from Hewitt et al. 1976). While Eggers (1976) modelled the energetics of planktivorous fish schools using the extensive literature on the feeding of individual fish, there is no experimental data on the feeding of fish schools to test such models. Without better data on the feeding of schooling fish on the zooplankton, contemporary models of marine zooplankton community dynamics have perforce concentrated upon interactions among the lower trophic levels (Steele 1974; Steele and Frost 1977).

I report here the results of in situ measure-

ments of the feeding selectivity of schools of *E. mordax* in the nearshore waters of the Southern California Bight. These represent the first direct quantitative field measurements of the feeding of schools of planktivorous fish.

## METHODS

A vessel with side-scanning sonar and echo sounder was used to track and determine the dimensions of large (25-200 t), near-surface schools of northern anchovy. A school was considered appropriate for study when 1) the school was near the surface and of sufficient size (>50 m along the axis perpendicular to the school's movement) that plankton samples could unequivocally be taken in its wake, 2) the school did not show signs of being disturbed by the ship's presence, and 3) the school was either directly observed to be feeding (October 1976) or its general configuration and movement were consistent with feeding behavior. It was assumed that when feeding, a school would either form an amorphous "ball" (Radakov 1973) or that its long axis would be normal to its axis of motion (Weihs 1973), and that the school's velocity would not exceed several body lengths per second.

When a school was selected for study, a cruciform drogue with surface buoy was dropped into its center. The school's movements in relation to the drogue were monitored for 10-25 min, during which time the school usually moved 100 to several hundred meters from the drogue. A weighted buoy was then placed over the school. Thus a transect was established, over which the school had passed while presumably feeding. The school's physical dimensions and swimming speed relative to the water could be determined using the ship's sonar, echo sounder, and by timing the school's movement between the two buoys.

In general, the sampling regimen consisted of taking two replicate samples with zooplankton nets first in the wake of the school between the buoys and then in "control" areas either in front of or several hundred meters to the side of the school. The nets were lowered obliquely from the surface to the average depth of the school (as determined by echo sounder), towed at that depth for 2 min, and then hauled to the surface (total length of tow about 100 m). A 0.5 m diameter plankton net (102  $\mu$ m mesh) with a TSK<sup>3</sup> flowmeter was towed in a harness with a 1.0 m

diameter (505  $\mu\text{m}$  mesh) net with a digital meter. Zooplankton samples were obtained successfully on four cruises conducted in the spring, summer, and fall of 1975-76. All sampling was conducted in daylight hours. Samples of the northern anchovy from the schools were taken by a commercial purse seiner on all but one cruise (April 1976) for positive species identification, analysis of their size composition, and examination of gut contents.

The sampling scheme varied slightly on several of the cruises: 1) The data from April 1976 represent the results of four replicate tows taken in the wake of the school and three control tows, rather than the two replicates taken for each set of tows on other cruises. 2) On the last cruise of October 1976, the concentration of plankton was measured before and after a school passed through a single patch of water. The control tows were taken first, directly in front of the school; the second set was obtained after the school had passed through the same area. 3) On the first cruise of August 1975, the 0.5 m diameter net was used alone. However, no large zooplankters were found in the samples from this cruise, and those collected were well within the net's range of maximal efficiency, as determined by comparison of catches from this net and the larger, 1 m net on subsequent cruises.

Analysis of the plankton samples consisted primarily of determining the size-frequency composition of the zooplankton in the wake of the school as compared with its composition in control tows. I selected for analysis dominant species from the major taxa of zooplankton occurring in the samples (i.e., copepods, chaetognaths, cladocerans, and larvaceans (Table 1)). Species were also selected on the basis of size, so that representatives of the smallest and largest commonly occurring zooplankters in each set of samples were enumerated. Following Cassie (1968), aliquot size was determined to count 20-50 organisms/size category; size categories with actual counts  $<10$  were lumped with the adjacent size category. Copepods were enumerated by life history stages, other organisms by body length. To facilitate comparison, results were converted whenever possible to micrograms carbon ( $\mu\text{g C}$ ) using conversions obtained from the literature for *Calanus* (Mullin and Brooks 1976), microcopepods (Landry 1976,

TABLE 1.—Plankton biomass and genera enumerated from control samples of plankton tows taken around northern anchovy schools in the nearshore zone of the Southern California Bight.

Cruise	Biomass <sub>3</sub> (mg C/m <sup>3</sup> )	Genera enumerated	
		Microzooplankton	Macrozooplankton
Aug. 1975	<sup>1</sup> 41	<i>Acartia</i> <i>Paracalanus</i> <i>Sagitta</i> ( $\leq 3$ mm) <i>Oikopleura</i>	None
8 Mar. 1976	<sup>2</sup> 663	<i>Evadne</i>	None
9 Mar.	<sup>2</sup> 639	<i>Evadne</i>	None
Apr.	<sup>1</sup> 33	<i>Acartia</i> <i>Sagitta</i> (0-3 mm)	<i>Calanus</i> <i>Sagitta</i> ( $\leq 12$ mm)
Oct.	<sup>3</sup> 10	<i>Acartia</i> Combined <i>Paracalanus</i> - <i>Clausocalanus</i> - <i>Ctenocalanus</i> Harpacticoids and cyclopoids	None

<sup>1</sup>Moderate.

<sup>2</sup>High.

<sup>3</sup>Low.

1978; Bartram et al.<sup>4</sup>), and *Sagitta* (Reeve 1970; Sameoto 1971). The total zooplankton biomass in the plankton samples was determined from displacement volumes of the samples taken with the 0.5 m diameter net; these values were converted to milligrams carbon per cubic meter ( $\text{mg C/m}^3$ ) (Wiebe et al. 1975).

## RESULTS

### Characteristics of Northern Anchovy Schools

The estimated biomass of the five schools studied ranged from 25 to 200 t (Table 2). The length of the schools (the dimension normal to the school's motion) varied by a factor of 4 (55-200 m). The breadth of the schools (the dimension parallel to the school's axis of motion) was generally less than their length and varied by less than a factor of 2 (30-55 m). The breadth of a feeding school, as a function of the number of fish from front to back, is critical to the degree the school depletes the plankton. The lesser variability in the breadth of the schools may result from behavioral regulation of this parameter, which determines the relative difference in feeding conditions encountered from front to back of the school. However, these data are inadequate to

<sup>3</sup>Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

<sup>4</sup>Bartram, W. C., D. M. Checkley, and J. F. Heinbokel. 1976. Further use of a deep tank in the study of the planktonic food chain. IMR Rep., IMR Ref. 76-7, p. 157-166. Institute of Marine Resources A-018, University of California, San Diego, La Jolla, CA 92093.

TABLE 2.—Characteristics of northern anchovy schools examined for feeding selectivity: overall school biomass, physical dimensions, velocity and prey consumption, number measured, and mean and range of standard lengths of *Engraulis mordax* within the schools.

Cruise	a Biomass (t wet wt.)	b Dimensions (m)			d Vertical	e Velocity (m/s)	f Plankton consumption (mg C/m <sup>3</sup> )	g Body wt. consumed/h <sup>1</sup> (%)	n	Standard length (mm)	
		Length	Front-back	Vertical						$\bar{x} \pm 95\%$ C.L.	Range
Aug. 1975	<sup>2</sup> 42	200	30	6	—	—	—	20	115.20 ± 5.02	96-139	
8 Mar. 1976	<sup>3</sup> 25	35	<sup>3</sup> 35	<sup>4</sup> 26	—	—	—	55	122.84 ± 29.17	83-148	
9 Mar.	<sup>3</sup> 50	55	<sup>4</sup> 55	20	0.29	—	—	16	98.25 ± 6.37	84-127	
Apr.	<sup>2</sup> 125	100	40	40	0.38	14.85	1.0	—	—	—	
Oct.	<sup>3</sup> 200	<sup>5</sup> 200	<sup>4</sup> 40	20	—	3.47	—	54	99.48 ± 1.52	90-144	

<sup>1</sup>Percentage body-weight consumed/h = [(volume swept clear/h)/(food removed/unit volume)/(school biomass)] × 100

= [π(0.5b)(0.5d)(e × 60<sup>3</sup>)(f × 10<sup>-3</sup>)/(a × 10<sup>6</sup> × 0.05)] × 100.

<sup>2</sup>Estimated from physical dimensions, density of 1.5 kg/m<sup>3</sup> (Hewitt et al. 1976), and assuming actual shape to be cylinder (August 1975) or oblate spheroid (April 1976).

<sup>3</sup>Fisherman's estimate based on purse seining of school.

<sup>4</sup>Back-calculated from tonnage, physical dimensions, and assumptions of average school density = 1.5 kg/m<sup>3</sup> and of a cylindrical (October 1976) or oblate spheroidal (March 1976) school shape.

<sup>5</sup>Estimate.

evaluate relations between feeding conditions and school size and configuration.

Samples of the northern anchovy were obtained from four of the schools. Two of the schools were composed of northern anchovies that had completed approximately 1 year's growth (98-99 mm SL); the other schools were composed of predominantly I-group (115 mm SL) and II-group (123 mm SL) northern anchovies (Table 2; Sakagawa and Kimura 1976). Since the schools composed of the largest and smallest fish were sampled under the same feeding conditions (i.e., the spring diatom bloom dominated by cladocerans of March 1976; Tables 1, 3), the feeding selectivity of large and small northern anchovies can be compared.

TABLE 3.—Ivlev's Electivity Index (*E*) as computed from the frequency of size classes of *Evadne* spp. examined in northern anchovy stomach contents and plankton tows taken in vicinity of the two schools sampled on 8 and 9 March 1976.

Date	Body length (μm)	Stomach samples (n = 10)		Plankton tows		<i>E</i> = (r-p)/(r+p)
		Total count	Proportion in ration (r)	Replicate sample counts	Proportion in tows (p)	
8 Mar.	200-299	9	0.036	44; 30	0.10	-0.47
	300-399	75	.30	145; 101	.33	-.05
	400-499	42	.17	132; 59	.26	-.21
	500-599	70	.28	83; 53	.18	.22
	600-699	37	.15	57; 33	.12	.11
	700-899	15	.060	2; 2	.0054	.83
	Total	248		741		
9 Mar.	200-299	4	.03	15; 14	.14	-.64
	300-399	10	.08	19; 13	.16	-.35
	400-499	30	.23	24; 15	.19	.09
	500-599	35	.27	42; 24	.32	-.10
	600-699	33	.25	23; 11	.17	.20
	>700	19	.15	4; 0	.02	.76
	Total	131		204		

### Feeding of Northern Anchovy Schools

The impact of the schools' feeding could be clearly determined from the plankton samples during all sampling periods except those of March

1976. In all 40 size categories of prey enumerated from August 1975 and April and October 1976 cruises, the median concentration was less in tows taken in the wake of the school than in control tows (Table 4). These data were analyzed as the fraction consumed [= 1 - (density of organisms in wake of school)/(density in controls)] as a function of the prey organisms' body size.

In computing regressions to analyze the feeding selectivity of the northern anchovy schools, it was often not clear either by eye, through analysis of residuals, or from the significance level of the regression whether a linear or curvilinear relationship best fit the data (Figure 1). In these instances, two regressions were performed: a linear regression and a regression in which the independent variable (i.e., prey body size) was log<sub>e</sub>-transformed. In computing the linear regressions (Figure 1), data points are excluded past the first size class at which the school has effectively consumed all the plankton (i.e., when consumption is >90%). An arcsine transformation was not performed, although it has been recommended for regressions performed on data expressed as fractions or percentages (Sokal and Rohlf 1969). The arcsine transformation did not significantly affect the form of the regressions presented below and only slightly enhanced their significance level. The data are therefore presented untransformed (Figure 1).

There was consistently a significant positive relationship between the fraction consumed and the size of the anchovy's prey on the cruises (Figure 1), despite the diversity of prey items within each cruise and the considerable differences in the composition and density of the zooplankton between cruises (Tables 1, 4). The fraction consumed ranged from 10-30% for the smallest organisms enumerated to 95-100% for

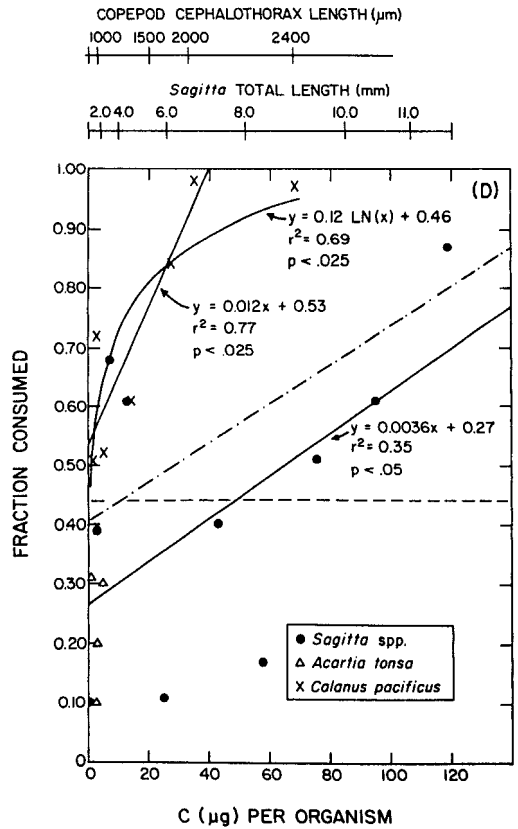
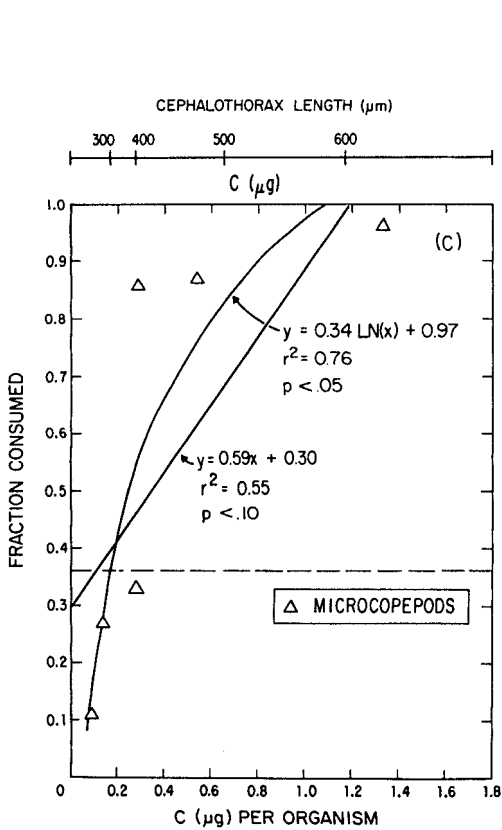
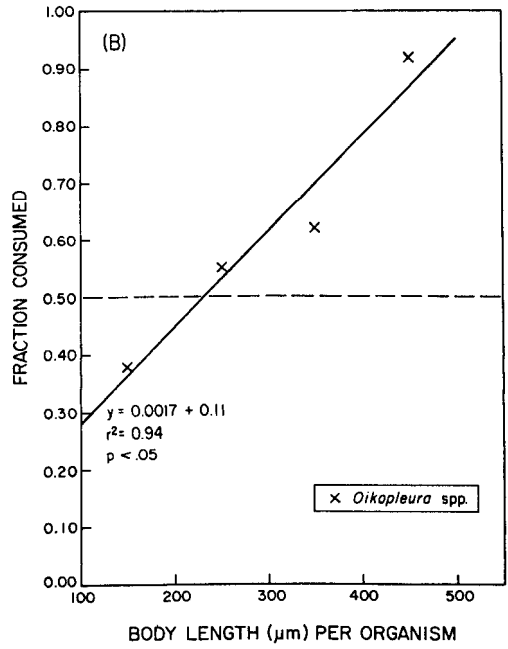
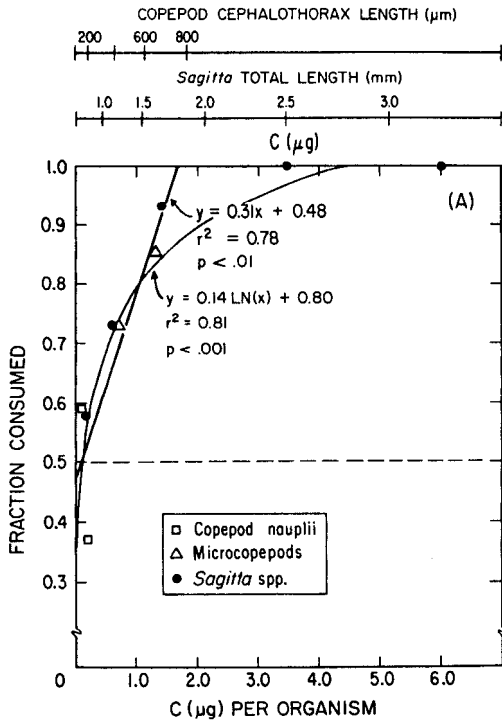
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TABLE 4.—Sample counts, density (numbers and biomass per cubic meter), and fraction consumed of prey items examined from control plankton tows and tows taken in the wake of northern anchovy schools, August 1975 and April and October 1976.

Prey organisms	Size class	Body weight (μg C)	Control tows				Behind-school tows				Fraction consumed
			Replicate sample counts	Abundance (no./m <sup>3</sup> )		Median biomass (μg C/m <sup>3</sup> )	Replicate sample counts	Abundance (no./m <sup>3</sup> )		Median biomass (μg C/m <sup>3</sup> )	
				Median	Range			Median	Range		
August:											
<i>Euterpina acutifrons</i>	Total Nauplii	0.10	128; 87	13,300	9,830-16,700	1,330	36; 45	5,430	5,370-5,500	543	0.59
<i>Acartia tonsa</i>	Total Nauplii	0.21	275; 302	35,000	34,100-35,900	7,360	135; 197	22,100	20,600-23,500	4,630	.37
<i>Paracalanus parvus</i>	CIII-VI	0.70	34; 53	209	178-240	165	9; 12	56.1	55.0-57.3	44.3	.73
<i>A. tonsa</i>	CIII-VI	1.35	136; 209	828	711-944	1,120	16; 31	122	97.7-148	166	.85
<i>Sagitta</i> spp.	500-999 μm	0.19	33; 11	111	49.7-172	21.1	12; 4	46.2	19.1-73.3	8.88	.58
	1,000-1,499 μm	0.62	264; 145	1,020	655-1,380	631	67; 31	279	148-409	173	.73
	1,500-1,999 μm	1.38	32; 20	129	90.4-167	178	2; 1	8.50	4.80-12.2	11.7	.93
	2,000-2,999 μm	3.42	14; 12	31.9	27.2-36.6	109	0; 0	0	.00-0.00	0	1.00
	>3,000 μm	6.08	9; 12	50.6	47.0-54.2	308	0; 0	0	.00-0.00	0	1.00
<i>Oikopleura</i> spp.	<200 μm		64; 22	217	99.4-334		27; 22	135	105-165		.38
(Trunk length)	200-299 μm		58; 51	267	230-303		25; 18	119	85.9-153		.55
	300-399 μm		15; 10	61.8	45.2-78.4		3; 6	23.5	18.3-28.6		.62
	>400 μm		6; 10	38.3	31.4-45.2		1; 0	3.10	.00-6.10		.92
April:											
<i>A. tonsa</i>	CI-IV	1.1	42; 38; 26	19.7	19.4-33.6	21.6	21; 15	13.6	13.1-14.1	15.0	.31
	CV	2.3	91; 34; 20	17.6	14.9-72.7	40.5	21; 20	15.8	14.1-17.5	36.4	.10
	CVI ♂	3.2	424; 279; 114	144	84.9-339	461	172; 130	115	114-116	368	.20
	CVI ♀	4.25	211; 294; 134	152	99.8-169	646	204; 85	106	74.5-137	451	.30
<i>Calanus pacificus</i>	CI	1.4	32; 203; 19	25.6	14.1-105	35.8	20; 13	12.4	11.4-13.4	17.4	.51
	CII	2.6	31; 173; 26	24.8	19.4-89.5	64.5	14; 5	6.89	4.38-9.40	17.9	.72
	CIII	4.9	44; 68; 30	35.2	22.3-35.2	172	31; 14	16.6	12.3-20.8	81.1	.52
	CIV <sup>1</sup>	14	481; 466; 297	30.9	27.8-46.6	433	137; 137; 164; 147	12.1	11.1-14.8	169	.61
	CV <sup>1</sup>	27	222; 136; 114	10.7	9.00-21.5	289	12; 16; 21; 34	1.69	.97-2.60	45.6	.84
	CVI ♂ <sup>1</sup>	35	55; 35; 46	4.31	2.32-5.33	151	1; 0; 2; 1	.08	.00-0.16	2.80	.98
	CVI ♀ <sup>1</sup>	68	45; 25; 27	2.53	1.66-4.36	172	1; 0; 1; 11	.08	.00-0.84	5.44	.97
<i>Sagitta</i> spp.	1.0-1.9 mm	0.96	29; 19; 54	23.2	9.8-40.2	22.3	16; 35	20.7	10.7-30.7	19.9	.11
	2.0-2.9 mm	3.22	43; 26; 40	29.8	13.4-34.4	96.0	31; 18	18.3	15.8-20.8	58.9	.39
	3.0-3.9 mm	7.13	33; 22; 23	17.1	11.4-26.4	122	7; 7	5.42	4.70-6.13	38.6	.68
	4.0-4.9 mm	12.9	16; 21; 9	12.8	6.70-10.9	165	11; 3	5.01	2.63-7.39	64.6	.61
	5.0-6.9 mm	25.5	16; 16; 9	8.28	6.70-12.8	211	9; 10	7.40	6.04-8.76	189	.11
	7.0-7.9 mm <sup>1</sup>	43	21; 19; 10	1.26	0.94-2.03	54.2	13; 10; 6; 2	.76	.15-1.08	32.7	.40
	8.0-8.9 mm <sup>1</sup>	58	30; 23; 10	1.52	0.94-2.91	88.2	15; 12; 13; 19	1.26	1.02-1.45	73.1	.17
	9.0-9.9 mm <sup>1</sup>	76	34; 47; 20	3.11	1.87-3.29	236	20; 12; 18; 34	1.52	1.30-2.60	116	.51
	10.0-10.9 mm <sup>1</sup>	95	47; 56; 35	3.71	3.28-4.55	352	25; 6; 14; 23	1.43	.65-2.03	136	.61
	≥11.0 mm <sup>1</sup>	119	35; 45; 21	2.98	1.97-3.39	355	9; 1; 3; 7	0.39	.11-0.73	46.4	.87
October:											
Harpacticoids and cyclopoids	100-299 μm	0.09	46; 34	585	476-694	52.6	70; 43	523	415-631	47.1	.11
	300-499 μm	0.28	12; 7	140	98.0-181	39.2	9; 11	93.6	81.1-106	26.2	.33
<i>A. tonsa</i> <sup>2</sup>	CI-II	0.29	92; 71; 62; 52	404	286-557	117	12; 16; 12; 21	57.4	45.1-81.0	16.6	.86
	CIII-VI	1.33	35; 23; 22; 12	135	66-211	180	0; 5; 0; 1	5.45	.00-18	7.25	.96
<i>Paracalanus-Clausocalanus-Ctenocalanus</i> <sup>2</sup>	CI-II	0.14	205; 184; 182; 259	1,190	1,003-1,424	167	262; 216; 260; 202	868	764-984	122	.27
	CIII-VI	0.54	48; 64; 92; 89	418	286-509	226	15; 21; 12; 12	55.6	45.4-75.7	30.0	.87

<sup>1</sup>Based on CalCOFI net tows.

<sup>2</sup>Sample counts for *A. tonsa* and combined *Paracalanus-Clausocalanus-Ctenocalanus* are presented in pairs, representing replicate counts from the same tows.



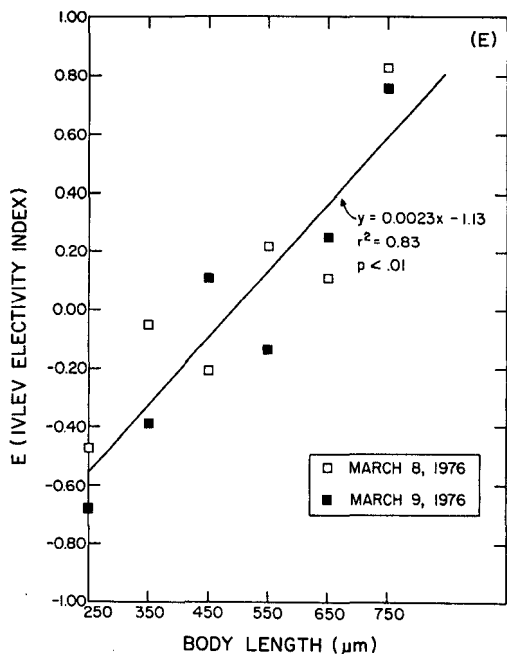


FIGURE 1.—Fraction consumed of zooplankton prey items by northern anchovy schools as a function of prey body size (A-D). Linear regressions were performed on all data sets, excluding from the regression data points past the first size class at which the school consumed >90% of prey. A curvilinear fit to the data based on a regression using a  $\log_e$ -transformation of values on the abscissa is shown where a curvilinear relationship provides as good or better fit. The regressions in Panels A-C include the data from each species found in the panel. In Panel D, the linear and curvilinear regressions in the upper left are based on data for *Calanus pacificus* alone; the solid lower regression is based upon data for *Sagitta* spp. and *Acartia tonsa*; the dashed oblique line is based upon the total data set for the sampling period. Dashed horizontal lines represent the fraction consumed of the total available zooplankton biomass. The significance level for each regression (which is also the significance level for each regression coefficient) is indicated. Panels: A and B—August 1975; C—October 1976; D—April 1976; E—March 1976: Ivlev's Electivity Index (E) as a function of the pigmented body length of *Evadne* spp.

the largest zooplankters (Table 4, Figure 1). Overall, the northern anchovy schools consumed 35-50% of the total available zooplankton in the areas sampled (Figure 1).

On the summer cruise (August 1975), a diverse assemblage of small plankton was present. Prey consumption appeared to be a function primarily of their size (expressed as their weight in micrograms carbon) (Figure 1A). A single regression, whether linear or curvilinear, adequately describes the northern anchovy's feeding selectivity for such morphologically dissimilar organisms as

copepod nauplii, *Euterpina acutifrons* and *Paracalanus parvus*; small calanoid copepodites, *Acartia tonsa* and *P. parvus*; and small chaetognaths, *Sagitta* spp. There is no indication of species preference. Nor is there evidence that prey density significantly influenced the rate at which they were consumed. While the relative concentration of similar-sized prey items varied widely, they were consumed at equivalent rates [Table 4, compare the density and consumption of copepod nauplii and *Sagitta* spp. (0.5-1.0 mm), *P. parvus* CIII-VI and *Sagitta* spp. (1.0-1.5 mm), and *A. tonsa* CIII-VI and *Sagitta* spp. (1.5-2.0 mm)].

The data for the northern anchovy's feeding on the larvacean, *Oikopleura* spp., from the August cruise was not directly comparable to data for the other species sampled at this time because their body length cannot be converted to a carbon value for the whole organism (including "house"). However, the northern anchovy's feeding on *Oikopleura* appeared to be a linear function of prey size (Figure 1B).

The autumn cruise (October 1976) was characterized by a low density of zooplankton—the standing crop was a factor of 3-4 less than that encountered during the April 1976 and August 1975 cruises—entirely dominated by small zooplankton as in the August 1975 cruise (Tables 1, 4). Again the northern anchovy's feeding selectivity was positively related to prey size (Figure 1C). A curvilinear relationship here provides a better fit to the data.

Only on the cruise of April 1976 were both large and small zooplankton present; however, the zooplankton density was comparable to that found on the summer cruise (August 1975) (Table 1, compare the range of the prey sizes; Table 5, compare Figure 1D with Figure 1A, C). As in the summer

TABLE 5.—Maximum prey size and its density, prey size at 100% consumption by northern anchovy schools as predicted from linear regressions, and slope of linear regressions of the school's feeding selectivity of prey size.

Item	April 1976			
	August 1975	<i>Calanus pacificus</i>	<i>Sagitta</i> spp. and <i>Acartia tonsa</i>	October 1976
Maximum prey size ( $\mu\text{g C}$ )	6.08	68.00	119.00	1.33
Concentration of largest prey item ( $\mu\text{g C}/\text{m}^3$ )	300	172	345	180
Predicted prey size ( $\mu\text{g C}$ ) at 100% consumption	1.68	39.20	203.00	1.19
Slope of regression of feeding selectivity	0.31	0.012	0.0036	0.59

cruise (August 1975), the school's feeding on both the small copepods, *A. tonsa*, and the chaetognath, *Sagitta* spp., increased as a single function of prey weight (Figure 1D). However, the school appeared to select the larger copepod, *Calanus pacificus*, over the other prey examined from this cruise. To test for the differential feeding selectivity for *C. pacificus*, a single linear regression was performed through the pooled data for prey consumption from the sampling period (Figure 1D) (Quade 1967). All data points for *C. pacificus* and only 3 of 14 data points for the consumption of *Sagitta* spp. and *A. tonsa* lie above this regression line, indicating a significantly heterogeneous distribution of the data ( $\chi^2 = 11.57$ ;  $P < 0.01$ ).

For the two sets of samples collected from two different schools on consecutive days during the March 1976 cruise, no significant differences were found between the control tows and those taken in the wake of the school either in the displacement volumes or in the plankton's size-frequency composition. This cruise was undertaken during an intense spring diatom bloom; ambient plankton concentrations were a factor of 20 greater than during any other cruise. At these plankton densities, northern anchovies could fill their stomachs [ca. 5% of body weight (Rojas de Mendiola and Ochoa 1973) for *Engraulis ringens* or 0.05 g C] in approximately 40 min by simple filtration (filtering rate per individual northern anchovy = 2 l/min (Leong and O'Connell 1969)). Thus, the schools, or some part of them, may have ceased feeding. Furthermore, at these high densities of plankton, the schools would have to ingest far more material than on the previous cruises to consume a detectable fraction of the plankton. The fish stomachs examined from both schools were full, but the data on the dimensions and biomass of the schools indicate they were not significantly more densely packed. The schools had thus apparently been feeding, at least intermittently, but under these conditions, their feeding selectivity could not be determined from the plankton samples alone.

To analyze the northern anchovy's feeding during this cruise, I compared the size-frequency composition of prey in the stomach contents with that found in the zooplankton tows (Table 3). The data were analyzed using Ivlev's Electivity Index:  $E = (r - p)/(r + p)$ , where  $r$  = the proportion the prey item represents in the diet and  $p$  = the proportion the prey represents in the plankton samples (Ivlev 1961).

The feeding of the northern anchovy on the cladocerans (predominantly *Evadne nordmanni*), which dominated the plankton during the spring bloom was a linear function of prey size (Figure 1E). No significant difference was found between the electivity of the two schools sampled under similar conditions of food density and composition on this cruise, although northern anchovies from the school of 8 March 1976 were the largest and those sampled on the following day were the smallest encountered during the study. Their difference in mean length ( $\bar{x} = 122.84$  and 98.25, respectively) indicates the schools were composed predominantly of II-group and 0-group fish, respectively, with a difference in mean weight of approximately a factor of 2 (calculated from Saka-gawa and Kimura 1976). But this difference in size apparently did not lead to a significant difference in their feeding selectivity under the sampling conditions.

#### Comparison of Feeding Selectivity Between Cruises

The three northern anchovy schools studied on the cruises of August 1975 and April and October 1976 each consumed approximately 100% of the largest prey available and a small fraction of the smaller prey. However, because the size distribution of available prey varied greatly between cruises, prey items that were almost entirely removed from the water when only small prey were available (e.g., the later copepodite stages of small copepods, such as *A. tonsa* or *P. parvus*, encountered during August 1975 or October 1976) were virtually ignored when larger prey were present (e.g., on the cruise of April 1976, compare Figure 1A, C with Figure 1D).

The prey size at which the northern anchovy school's consumption was approximately 100% on these three cruises (which may be defined as the intersection of the linear regressions with the line  $y = 1$ ) varied by more than a factor of 100 (Table 5; Figure 1A, C, D). Furthermore, while the school's feeding selectivity was consistently a positive function of the prey's size, the slopes of the linear regressions from the cruises of August 1975 and April and October 1976 also varied by more than two orders of magnitude (Table 5). Both factors are related to the size range of prey available to the anchovy on these cruises, which varied to a similar degree.

There is a positive relation between the prey



size at which the anchovy school's consumption is about 100% and the size of the largest plankters enumerated (Figure 2A). The northern anchovy apparently adjusts its feeding so that it continues to select the largest prey over at least a hundred fold range in prey size. (It should perhaps be noted that the largest commonly occurring zooplankters were counted in all samples, and all were found in median concentrations of 172-345  $\mu\text{g C/m}^3$  (Table 5).) While less common, larger zooplankters may

have occurred in the samples or at the sample sites, relatively rare individual prey items probably would not affect the feeding pattern of a planktivore, such as the northern anchovy.)

Similarly, the slope of the northern anchovy schools' feeding selectivity is a positive function of the inverse of the largest prey sizes occurring in the samples (Figure 2B), since  $m = \Delta y / \Delta x \cong 1/x_L$ , where  $m$  = the slope of the school's feeding selectivity;  $\Delta y$  = the difference between the fraction consumed of the largest and smallest prey ( $\cong 1$ );  $\Delta x$  = the range ( $\omega$ ) in size of the prey organisms; and where the size of the largest prey,  $x_L \gg x_s$ , the size of the smallest prey. For this limited set of observations, the relation between the slope of the schools' feeding selectivity ( $m$ ), in fact, appears inversely proportional to the size of the largest prey available ( $x_L$ ): the coefficient of the regression between  $m$  and  $1/x_L$  is about 1 (Figure 2B). Stated another way, the northern anchovy schools' feeding selectivity over a range of conditions was related to the size of the largest prey available in significant quantity. The largest prey may be considered to be entirely consumed, and the consumption of smaller prey is approximately proportional to their size in relation to the largest prey.

## DISCUSSION

### Evaluation of the Field Method

There are several possible biases to the field sampling method: 1) Its accuracy depends upon the choice of control samples. It is clearly preferable to sample a patch of water both before and after a school has passed through it. However, bias due to small-scale patchiness in selecting control samples on the sides of the school's path will probably lead to conservative estimates of prey consumption, since the school will presumably swim through the richest plankton patches. 2) The method would be biased to the extent that the disappearance of zooplankters in the wake of the school resulted from escape from the school rather than their consumption by it. However, this does not appear to be a significant problem, considering the large size of the fish schools sampled in this study. The range of swimming speeds of copepods is on the order of 5-50 body lengths/s (ca. 0.5-5.0 cm/s) (Enright 1977). The northern anchovy schools sampled were on the order of 50-200 m in length, 10-40 m in depth, and advanced at about 10-40 cm/s. Unless the zooplankters could detect

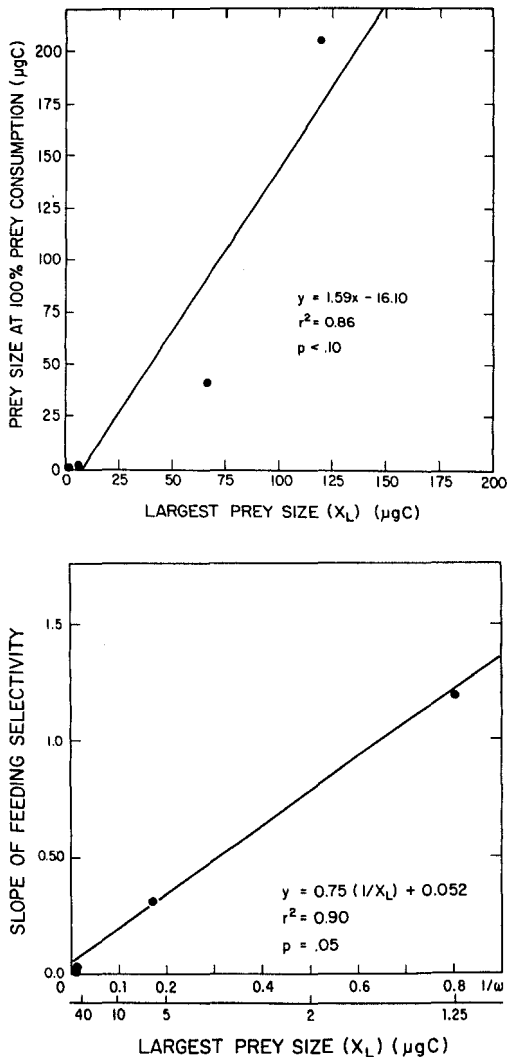


FIGURE 2.—(A) Predicted prey size at 100% prey consumption and (B) slope of feeding selectivity of northern anchovy schools (from Figure 1) as a function of, respectively, the largest prey size and the inverse of the largest prey size available in significant quantity. (See Table 4 and text for detailed explanation.)

the school from a considerable distance, which seems unlikely, they could not escape it.

There are also advantages to the direct field sampling method: 1) It circumvents uncertainties attendant upon extrapolating from laboratory to field conditions. 2) It avoids the bias inherent in the use of fish stomachs, due to the differential digestibility of various prey organisms. This can significantly bias estimation of selective predation (e.g., see Gannon 1976). 3) It permits study of far larger aggregations than can be accommodated in the laboratory. In the Southern California Bight, approximately 90% of the biomass of the northern anchovy population is found in schools >25 t (calculated from Hewitt et al. 1976)—the size of the schools sampled in this study.

More generally, the feeding of planktivorous fish has hitherto been studied experimentally using individual or small groups of fish (Ivlev 1961; Beukema 1968; Leong and O'Connell 1969; O'Connell 1972; Ware 1972; Werner and Hall 1974; Confer and Blades 1975; O'Brien et al. 1976). Prey selectivity was analyzed as a complex function requiring understanding of the predator's metabolic state and the prey's size, density, and patchiness. It is an awesome, if not impossible, task to extrapolate this analysis to field situations involving  $10^2$ - $10^7$  predators interacting within a school as they feed upon natural prey assemblages.

A field-oriented approach permits study of the feeding of fish schools from the perspective of a higher level of organization, as well as permitting a test of laboratory studies. Viewing the method in this context, it is important to note the close replication of results in the instance in which it was successfully repeated under a similar set of field conditions (March 1976, Figure 1E). The median significance level of the regressions (and the regression coefficients) in Figure 1 was also quite high ( $P < 0.025$ ), despite the relatively few data points on which the regressions are based and the nature of the data, which is derived from field sampling of zooplankton. The feeding of fish within large schools is sufficiently consistent that significant proportions of the variance in plankton distributions in the wake of the schools can be explained in terms of their impact.

### Comparison with Other Studies

The results of the present study appear consistent in broad outline with the pattern of size-

selective feeding noted in laboratory studies; i.e., prey selectivity proved a function of prey size rather than of their taxonomy (Ware 1972; O'Brien et al. 1976). This was found for a range of prey sizes and taxa (Figure 1, Table 4). Significantly enhanced consumption of a particular species was observed only once; i.e., for *Calanus* during the April 1976 cruise (Figure 1D). Since *Calanus* was encountered only on this cruise, it is not clear how much significance should be attached to this finding.

This study indicates it may be possible to predict the feeding selectivity of northern anchovy schools on the basis of data on the size of prey available to the school in significant quantity; i.e., both the slope of the northern anchovy's feeding selectivity and the size of the prey that will effectively be removed entirely from the water is a function of the largest available prey (Figure 2). This result is attractive, since data on the size distribution of the zooplankton can now be collected on a routine, continuous basis (Mackas and Boyd 1979; Herman and Dauphinee 1980).

However, experimental studies have often found that the concentrations of individual prey items significantly influence the feeding selectivity of fish (Ivlev 1961; Beukema 1968; O'Connell 1972; Ware 1972). This is presumably mediated through the varying degrees of experience the predator will have with prey at different densities. However, prey density did not appear to be a significant factor in determining the northern anchovy's prey selectivity in this study. On both the August 1975 and April 1976 cruises, small copepods and chaetognaths of equivalent body weight were consumed in approximately equal proportions (Figure 1A, D), although their relative densities frequently varied by a factor of 5 or greater (Table 4). Nor can prey density be invoked to explain the anchovy's heightened selectivity for *Calanus* (Figure 1D). The density of *Calanus* (April 1976) did not appear to differ significantly from the density of *Acartia* and *Sagitta* of similar size that were consumed to a lesser degree (Table 4).

This apparent difference between experimental and field results may arise from significant differences in the distribution of prey typically available in the two situations. In laboratory studies examining the influence of prey density on feeding selectivity, the fish are typically offered several prey items at varying densities (Ivlev 1961; Beukema 1968; O'Connell 1972; Ware 1972). Under

such conditions, the predator may form a "search image" for a particular prey item (Tinbergen 1960; also as discussed by Beukema 1968). However, planktivorous fish in marine systems typically have a wide variety of prey items available to them. Furthermore, the relative densities of different zooplankters available to the fish will vary constantly due to vertical and horizontal patchiness of the plankters' distribution, the movements of the school, and the very differences from front to back of the school created by its feeding. Thus, under most natural conditions, it may not be feasible for planktivorous marine fish to form "search images" and to select particular prey items based upon their relative abundance in the environment.

Further quantitative field studies on the feeding of marine schooling fish should enhance our understanding of the role of these planktivores in pelagic ecosystems. Particular questions to be addressed include 1) the role their feeding plays in regulating the structure of marine plankton communities, and 2) the degree to which fish populations themselves are regulated by inter- and intra-specific predation upon the early life stages. It should also be possible to study 3) the relation between planktonic conditions and the distribution and schooling behavior of planktivorous fish, which is no doubt linked to their availability to commercial fishing operations.

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