

A LABORATORY STUDY OF PARTICULATE AND FILTER FEEDING OF THE PACIFIC MACKEREL, *SCOMBER JAPONICUS*

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ABSTRACT

In laboratory feeding trials Pacific mackerel, *Scomber japonicus*, averaging 147 g in weight did not respond to *Artemia* nauplii, but did capture *Artemia* adults by biting (particulate feeding) when density was 1 or 2/liter and by filtering when density was 22 to 112/liter. Particulate feeding is described by $N_p = 60.3tD$, where N is the number of *Artemia* ingested in t minutes at D numbers per liter. Filter feeding is described by $N_F = 23,788 (1 - e^{-0.0036t\sqrt{D}})$, where 23,788 is an asymptotic estimate of the number of *Artemia* in the digestive tract at full capacity.

The results suggest that the mackerel utilizes only the larger of the planktonic crustaceans, such as euphausiids, in the sea. For the relatively low average densities of such organisms the derived equations indicate that the mackerel could not obtain its daily nutritional requirement, estimated to be 8% of body weight, in less than 24 hr of feeding. Though the daily requirement could be obtained in much shorter periods, perhaps by filter feeding, if such crustaceans are encountered in aggregations of considerably higher density than reflected by area averages, it is probable that the mackerel must often depend in part on such larger organisms as fish to fulfill its needs.

Comparison of the mackerel ingestion rates to those for the smaller northern anchovy indicates that while the individual mackerel may generally capture a greater proportion of the large crustaceans encountered than the anchovy, the proportion captured would have a relatively lower nutritional value for the mackerel.

The Pacific mackerel, *Scomber japonicus*, is one of several pelagic schooling fishes of the eastern temperate Pacific which feed on zooplankton, but it does not depend entirely on zooplankton. Fitch (1956) reported that stomach contents contained about 30% larval and juvenile fish by volume, with the remainder composed largely of such crustaceans as mysids, copepods, and euphausiids. Frey (1971) commented that larval and juvenile fish appear to be the most important food, but that the mackerel relies heavily on euphausiids at times. Hatanaka et al. (1957) showed that *S. japonicus* in coastal regions of Japan consume mainly small anchovies in the late summer and autumn and euphausiids in other seasons. The biomass of euphausiids con-

sumed annually was estimated to be three or four times that of anchovies.

In addition to being the dominant element in the diet of *S. japonicus*, the larger crustaceans are an important class of food for a number of other pelagic schooling fishes. The jack mackerel (*Trachurus symmetricus*) is known to feed heavily on small fish and squid at times (Fitch, 1965), but about 70% of stomach contents by volume is euphausiids (Carlisle, 1971). The Pacific sardine (*Sardinops caerulea*) feeds largely on copepods smaller than those consumed by the jack mackerel but is occasionally gorged on euphausiids, and these average about 5% of stomach contents by volume (Carlisle, 1971). The northern anchovy (*Engraulis mordax*) consumes phytoplankters and small zooplankters, but large copepods and euphausiids appear to be the most important food items (Loukashkin, 1970). Thus while all of these species prey on

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large crustaceans, the latter do not necessarily make an equivalent contribution to their diets. It is probable that the segment of the biota represented by such crustaceans in the sea is a food source of different potential for different fishes.

Assessing the food potential of large crustaceans for the Pacific mackerel, or any of the above teleosts, requires a knowledge of the density levels of such crustaceans in the sea and of the rates at which the organisms can be captured in relation to density. Leong and O'Connell (1969) determined by a laboratory study the rates at which the northern anchovy feeds on *Artemia* nauplii by filtering and on *Artemia* adults by biting (particulate feeding), and O'Connell (1972) showed that the two kinds of feeding activity in a small school varied with the relative abundance of the two sizes of *Artemia*. The present study was undertaken to obtain comparable information for the Pacific mackerel, using *Artemia* as the food. The results are discussed in respect to the densities of large crustaceans in the sea and in respect to the feeding rates of the anchovy.

METHODS

Feeding trials were carried out in an arrangement of two plastic pools with a connecting trough and gates (Leong and O'Connell, 1969; O'Connell, 1972). The pools were supplied with a continuous flow of filtered sea water and each contained 4.5 m³ of water at a depth of 0.61 m (2 ft). They were under a 12-hr day, 12-hr night cycle of illumination, but all trials were carried out during the day. Temperature varied from 16° to 19°C.

A school of about 160 mackerel was acclimated in the pool arrangement with the gates open for about 2 weeks and then confined to one pool before the study started. The fish averaged 222 mm (202 to 247 mm) in standard length and 152 g (100 to 225 g) in weight. The latter average is based on weights taken at the end of each feeding trial and included digestive tract contents, which were later found to range from 0.1 to 21.8 g. These values were subtracted from the measured fish weights to obtain estimates

of the weights before feeding. The subsequent analysis involves the adjusted weights, which averaged 147.3 g.

All feeding trials were preceded by at least 24 hr without feeding, which was enough to produce virtually empty digestive tracts in preliminary investigations. For each trial the water flow was turned off, and four fish were diverted from the holding pool to the trough and then admitted to the prepared food situation in the other pool where they were allowed to feed for a given number of minutes. Closing of the gate after admission initiated the time period and introduction of a hinged crowder, which was rapidly closed to trap and remove the fish, terminated the time period. The fish were killed in less than 2 min after introduction of the crowder, immediately measured and weighed, then placed in jars of 10% Formalin with the body cavity opened.

Though the study is concerned primarily with feeding on *Artemia* adults, a few feeding trials were carried out with newly hatched *Artemia* nauplii, which averaged 0.65 mm in length, to document the response of the mackerel to very small crustaceans. The densities in the water were estimated from subsamples, and quantities in the digestive tracts were estimated by total counts or volumetric aliquoting, as described by Leong and O'Connell (1969).

Feeding on *Artemia* adults is based on digestive tract contents of four fish in each of 28 trials, with each trial representing a different combination of food density and feeding time (Table 1). The food situation was established for each trial by placing a given wet weight of *Artemia* adults in the experimental pool and dispersing it gently with wide-mesh dip nets just before admitting the fish. The weights given under food quantity are the wet weights introduced at the start of each trial. These were selected after preliminary observation to include the highest and the lowest levels that could be managed conveniently. The multiplication factors given in certain cells of the table indicate the number of times the specified weight was introduced into the pool during the trial, e.g., 20 g was introduced six times, or at 15-min intervals, during the 90-min trial. This was done to sustain the nominal food den-

TABLE 1.—The array of trials with respect to food density and feeding duration. Number/liter is the nominal density for the weight introduced.

Quantity of <i>Artemia</i>		Minutes of feeding					
Total weight	Number liter	2.5	5	10	30	60	90
g							
10	1	1	1	1	1(3×) ¹	1(6×)	1(9×)
20	2	1	1	1	1(2×)	1(4×)	1(6×)
200	22	1	1	1	1	1	1
590	66	1	1	1	1	1	1
1,010	112	1	1	1	1	--	--

¹ The multiplication factors show the number of times, at equal intervals, that the specified weight was introduced during the trial to maintain the nominal density. See text.

sity over long periods at the lower food density levels. Introduction of food during the trial, and even brief dispersion with the wide-mesh net, did not appear to distress the fish and scarcely interrupted their feeding activity.

The intervals of food introduction for the lower density levels were determined from a preliminary study. During a 30-min trial with 20 g of *Artemia*, e.g., feeding activity declined sharply after 15 min, and average digestive tract contents did not differ from that for a trial of 15 min. A trial of 30 min with two introductions of 20 g showed approximately double the digestive tract contents of the above two. The 10-min interval for 10 g introductions was established from similar considerations. Food availability remained high throughout the trials at the three higher density levels.

The nominal densities of *Artemia* shown in Table 1 are based on the volume of the pool and a conversion factor of 500 *Artemia* adults/g wet weight. The conversion factor is an average derived from samples from the several batches of *Artemia* delivered to the aquarium. Portions of these samples also indicated that individuals averaged 4.5 mm in length and 0.48 mg dry weight.

The quantities of *Artemia* in the digestive tracts of the fish were estimated separately for the mouth, the esophagus and stomach combined, and the anterior and posterior halves of the intestine. The contents of the esophagus and stomach were weighed. Numbers in the various sections were estimated by total count where quantity was low, but by counts from aliquots where the quantity was large. These data indi-

cated that the weight of ingested *Artemia*, determined 2 to 6 months after preservation, was 25 to 50% lower than the weight of the live organisms. Digestion and leaching by Formalin may have been responsible for such loss. Since the weights of food in the digestive tracts could not be considered representative of the weights of food consumed, the analysis was carried out on the numbers of organisms in digestive tracts.

Values for all sections of the digestive tract were pooled to obtain estimates of total digestive tract contents, the primary entity in analysis. The numbers found in the mouth varied from less than 1 to 53% and averaged 18% of total digestive tract contents. This percentage, furthermore, varied with food density, increasing from 4% at the 10 g level to 41% at the 1,010 g level. It is presumed that the contents of the mouth were accumulations to be swallowed and/or material regurgitated during capture. Proportions in the intestine were considerably lower and will be described later.

RESULTS

RESPONSE TO ARTEMIA NAUPLII

Three trials were carried out with newly hatched *Artemia* nauplii as the only available food. In two cases the average densities of nauplii were about 190/liter and 230/liter, and groups of four fish showed no recognizable feeding activity during 30-min periods of exposure. In the third case density was a little more than 200/liter and a group of approximately 50 fish showed no feeding activity. The stomachs of five fish from these trials contained no nauplii, although a few nauplii were found on the gill rakers of two of them.

One trial was carried out with *Artemia* adults and nauplii both present in the water. The density of adults was 22/liter and the density of nauplii was 185/liter. After feeding for 5 min, four fish averaged 2,334 *Artemia* adults and 823 *Artemia* nauplii (635 to 1,083) in the mouth, stomach, and esophagus combined. The bulk of both sizes of organism was in the stomachs.

From these results it is evident that while the Pacific mackerel did not respond to nauplii alone,

it did ingest them along with the larger *Artemia* when both were present in the water. However, the dry weight of the nauplii ingested would be about 0.1% of the dry weight of the adults ingested. It appears, also, that the uptake of nauplii was only about 4% as efficient as the uptake of adult *Artemia*, i.e., the number of nauplii per fish represents 4.4 liters of water in the pool, while the number of adults per fish represents 106 liters.

Yasuda (1963) obtained results comparable to the above for *S. japonicus* 120 to 130 mm in length. He found that the mackerel did not eat brine shrimp (0.38 mm in length and presumably nauplii) as did anchovies (*Engraulis japonica*) and even horse mackerel (*Trachurus japonicus*) of approximately the same length. The spacing between gill rakers and gill raker processes was shown to be smaller in the latter two species than in the Pacific mackerel.

RESPONSE TO ARTEMIA ADULTS

The 28 trials in which *Artemia* adults were the only available food showed that feeding was particulate at the two lower density levels and filtering at the three higher density levels. Particulate feeding is the capture of individual organisms by directed biting. Filter feeding is the process of straining organisms from the water as it passes through the gill rakers while the mouth remains open. The duration of mouth opening was 1 to 3 sec, and such mouth openings occurred almost rhythmically 15 to 20 times/min. Filtering, however, was sustained for only a limited time, and this time varied inversely with density level of the food. It lasted 30 min at 22 *Artemia*/liter, 20 min at 66 *Artemia*/liter, and about 15 min at 112 *Artemia*/liter. At these times the fish noticeably reduced swimming speed and shifted to particulate feeding. Though particulate feeding appeared to be less vigorous under these circumstances than at the two lowest food densities, complete cessation of feeding did not occur in any of the trials.

The trial groups of four fish evidenced some discomfort upon encountering the highest food density, 112 *Artemia*/liter. Swimming speed

and coloration showed less increase than at other densities, and filtering intervals were shorter and less rhythmic. A school of about 70 fish introduced to this highest density, on the other hand, exhibited strong rhythmic filtering accompanied by marked intensification of color and increased swimming speed. Though digestive tract contents from the fish of this group were not significantly greater than for the four-fish group after 5 min of feeding, the larger group virtually eliminated the available food in this time while the smaller group did not noticeably affect its density.

Preliminary analysis indicated that there was no confounding of size of fish with density levels and suggested that the larger fish tended to consume slightly more food at all densities. Hence, estimates of total digestive tract quantities were standardized to the average adjusted weight of all fish (147.3 g) by simple proportion. The means and standard errors of the standardized numbers are shown for each trial in Table 2. The greatest change in a trial average resulting from standardization was 20% of the original estimate, and the change was 5% or less for half of the trials. Standardization also affected the estimates of variability, but only to the extent that the coefficients of variation averaged 1% higher.

A separate analysis for each of the food density levels indicated that digestive tract contents increased proportionately with time at the two lower densities, but increased exponentially toward an asymptotic value at the three higher densities. It was also evident that the density-specific rates of increase varied directly with density for the two lower levels and with the square root of density for the three higher levels. The modes of food accumulation for the two density ranges can therefore be expressed as

$$N_P = \alpha t D \quad (1)$$

and
$$N_F = N_\infty \left(1 - e^{-\beta t \sqrt{D}} \right) \quad (2)$$

where N_P = number of organisms in the digestive tract after t minutes of particulate feeding,

TABLE 2.—The average fish weight and the mean (\bar{X}) and standard error (SE) of the standardized number of *Artemia* in the digestive tract for each trial.

Density Number/ liter	Feeding duration min	Number fish	Average fish weight g	Number in digestive tract	
				\bar{X}	SE
1	2.5	4	125	149	60
	5	4	130	299	168
	10	4	136	572	86
	30	4	134	2,280	373
	60	3	135	3,430	342
	90	4	150	5,620	216
2	2.5	4	149	254	37
	5	4	148	695	81
	10	3	149	1,530	163
	30	4	123	4,636	583
	60	4	157	5,790	684
	90	4	149	11,325	1,204
22	2.5	2	136	745	263
	5	4	159	2,013	101
	10	3	141	4,399	270
	30	3	135	10,893	790
	60	4	165	15,664	648
	90	4	152	18,079	1,143
66	2.5	3	159	1,502	197
	5	3	139	4,041	409
	10	4	158	5,232	858
	30	4	174	9,863	990
	60	4	158	12,676	484
	90	4	168	15,723	605
112	2.5	3	145	3,079	936
	5	3	155	3,617	447
	10	4	139	7,629	982
	30	4	147	15,845	2,600

N_F = number of organisms in the digestive tract after t minutes of filter feeding,

D = the nominal density of food in numbers per liter,

N_∞ = asymptotic number of organisms in the digestive tract at full capacity,

α = specific feeding rate, and

β = instantaneous feeding rate.

Fitting all of the data in the two low density series with equation (1) and those in the three high density series with equation (2) resulted in a satisfactory fit for the low density group but not for the high density group. Calculated values tended to be lower than trial values for the 22 *Artemia*/liter series, and higher than trial values for the 66 *Artemia*/liter series, particularly for the longer time periods. The difficulty arises from the fact that average quantities in

the digestive tracts were lower for the 66 *Artemia*/liter level than for the 22 *Artemia*/liter level in the 30-, 60-, and 90-min trials. The reason for this is not known, but examination of the quantities in the anterior and posterior halves of the intestine for all trials (Table 3) offers a plausible explanation.

TABLE 3.—Average number of *Artemia* in anterior (A) and posterior (P) halves of intestine for each trial.

Time	Density				
	1	2	22	66	112
2.5 A	0	15	9	33	300
P	0	0	0	0	0
5.0 A	0.3	15	108	101	175
P	0	0	0	0	0
10 A	1.8	50	57	215	467
P	0	0	0	10	59
30 A	50	51	320	1,077	1,265
P	0	0	36	327	245
60 A	0.7	165	830	569	
P	0	45	720	714	
90 A	141	209	890	937	
P	4	339	385	722	

At 22 *Artemia*/liter the maximum quantity in the intestine is reached at 60 min, and at 66 *Artemia*/liter the maximum is reached at 30 min. Fluctuations in the two halves of the intestine thereafter suggest posterior movement of material and intermittent elimination. This is corroborated by visual observations made during the trials. The earliest detected defecations were at 50 min for the 22 *Artemia*/liter level and at about 30 min for the 66 *Artemia*/liter level. No defecation was detected in the trials at 112 *Artemia*/liter, which did not go beyond 30 min. The quantities in the intestine suggest that rate of movement of material into the posterior part of the intestine approached the maximum at 66 *Artemia*/liter and that defecation might not start any sooner at 112 *Artemia*/liter than at 66 *Artemia*/liter.

From these data it is reasonable to suppose that beyond 30 min the time-specific losses by defecation would be greater for the 66 *Artemia*/liter series than for the 22 *Artemia*/liter series, and negligible for the two lower density levels.

On the supposition that the greatest underestimates of total amounts consumed occurred in the three longest time periods of the 66 *Artemia*/liter series, equation (3) was refitted to

TABLE 4.—Estimated parameter values and 95% confidence limits for density series separately and pooled under particulate and filter feeding.

Artemia/liter	Particulate feeding	
	Intercept	Slope (α)
1	46.8 (-316; 410)	61.5 (53.5; 69.5)
2	181.3 (-1,004; 1,367)	58.5 (45.9; 71.1)
Pooled	0 assumed	60.3 (56.3; 64.3)
Artemia/liter	Filter feeding	
	Asymptote (N_{∞})	Instantaneous feeding rate (β)
22	20,322 (16,736; 23,908)	0.0052 (0.0031; 0.0074)
66	15,384 (13,991; 16,778)	0.0045 (0.0035; 0.0060)
112	22,050 (16,999; 27,102)	0.0040 (0.0029; 0.0059)
Pooled ¹	23,788 (21,802; 25,775)	0.0036 (0.0032; 0.0042)

¹ The pooled array under filter feeding does not include the 30-, 60-, and 90-min trials for 66 *Artemia*/liter.

the data for the higher density levels with these three trials removed. The estimated parameters are shown, along with those for the lower density levels, and also for the density levels individually, in Table 4. Since the individual series under particulate feeding did not have intercepts that differed from zero, the parameters for the pooled array were estimated with the intercept assumed to be zero. Goodness of fit for the combined data in both density groups was judged satisfactory; in Figure 1 the calculated curves are compared to the standardized trial means and standard errors for each density series. The equations for the two feeding modes can be stated as

$$N_P = 60.3tD \quad (3)$$

$$\text{and} \quad N_F = 23,788 \left(1 - e^{-0.0036t/D}\right) \quad (4)$$

The asymptotic level, 23,788 *Artemia*, is indicative of the maximum capacity of mackerels at an average weight of 147 g. On the basis of the wet weight of *Artemia*, 500 individuals/g, maximum capacity would be 48 g, or 32% of fish weight. This is about double the greatest weight of fish food removed from the esophagus and stomach, but the two kinds of estimate are not necessarily inconsistent. As suggested earlier, the weights of the digestive tract contents may have underestimated the weights of *Artemia* in the live state by 25 to 50% because of digestion and leaching in Formalin. The estimate given here is based on weight of live organisms. Since digestion is going on during protracted feeding,

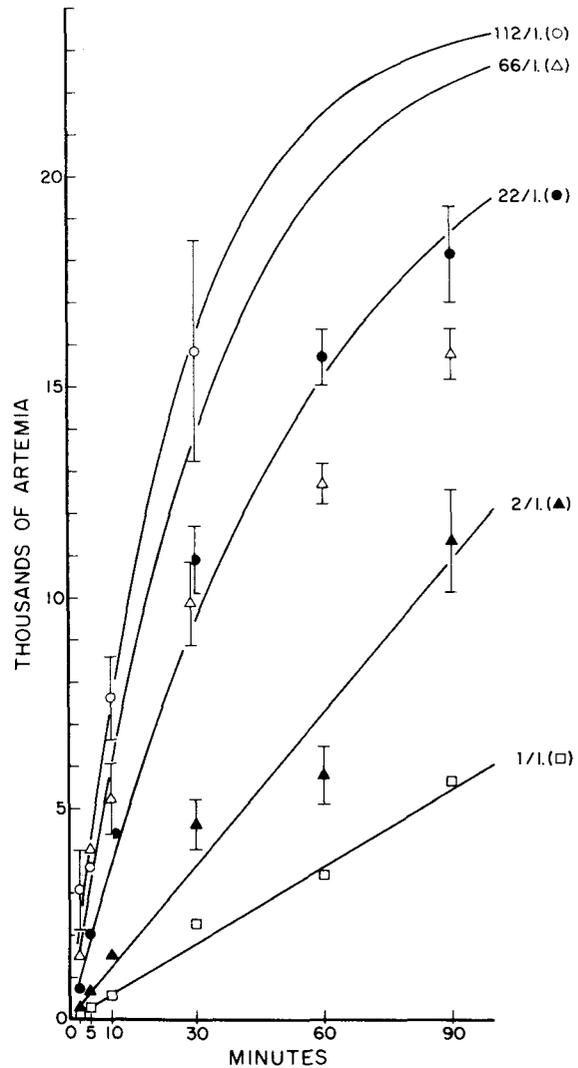


FIGURE 1.—The number of *Artemia* in digestive tracts for different density levels in the water and for different feeding durations. The lines for 1 and 2 *Artemia*/liter were calculated from equation (3) and the lines for 22, 66, and 112 *Artemia*/liter were calculated from equation (4). The symbols associated with each line show averages and standard errors for the trials in that density series. Standard errors smaller than 450 are not shown.

average capacity might well be less than 32% of weight for the asymptotic number specified. The asymptotic number, which was most strongly influenced by the trials at 22 *Artemia*/liter, may slightly underestimate the total number that can be ingested because of losses by defecation.

DISCUSSION

It is evident that *Artemia* adults approximate the smaller crustacean sizes utilized by the mackerel and that the fish resorts to filter feeding to increase the rate of consumption as density exceeds some level where particulate feeding becomes relatively inefficient. The ecological meaning of this feeding pattern is indicated by considering the resulting relation between food density and rate of food accumulation in the digestive tracts in respect to 1) the daily nutritional requirement of the species, 2) the density levels of crustaceans in the sea, and 3) the feeding rates of the northern anchovy (*Engraulis mordax*).

Hatanaka et al. (1957) showed that *S. japonicus* in coastal regions of Japan tend to utilize small fish in late summer and autumn but to rely largely on euphausiids and other crustaceans of similar size in other seasons. They concluded that mackerel a little over 1-year-old and averaging 149 g in weight required 8% of their body weight per day in crustaceans to sustain the growth rate observed in nature, which was estimated as 0.42% of body weight per day. The feeding functions derived in the present study indicate that the times required for the mackerel to obtain this daily requirement at the *Artemia* densities tested, or their equivalent for euphausiids, would be

<i>Artemia</i> /liter	1	2	22	66	112
Euphausiids/liter	0.7	1.3	15	44	75
Minutes	97	49	17	10	7

The equivalent densities for euphausiids are given on the assumption that the mackerel feeding rate is keyed to concentration in terms of biomass rather than to numbers per unit volume as such. Euphausiids near the surface at night in the eastern Pacific, largely *Euphausia pacifica*,

average 6 mm in body length (O'Connell, 1971), and individuals of this length are 3 mg wet weight (Lasker, 1966), or 50% more than the *Artemia*.

The feeding times given above are relatively short, but the *Artemia* densities are much higher than those reported for comparable organisms in the sea. Brinton (1962) showed average densities of *E. pacifica*, largely juveniles, to be about 0.02/liter near the surface at night off southern California. O'Connell (1971) showed an average of 0.03/liter over much the same region, with perhaps 5 to 10% of the area having densities approaching 0.1/liter at any one time. These estimates would be elevated, perhaps doubled, if other large crustaceans were added on a biomass equivalent basis. The highest of these area densities would enable the mackerel to obtain its daily nutritional requirement in about half a day of particulate feeding, but the more commonly prevailing level would not permit the mackerel to obtain its requirement within the space of a day.

In all probability the mackerel obtains much of its needs from euphausiids and other crustaceans of similar size, but there is good evidence that it depends to some extent on larger organisms, such as fish up to one-third of its own body length (Hatanaka and Takahashi, 1960), to secure the daily requirement over a reasonable length of time. Though stomachs tended to be fuller and growth better during the season when the mackerel feeds primarily on fish (Hatanaka et al., 1957), it must be remembered that the 8% daily feeding requirement used here pertains to maintenance and growth when euphausiids were the primary food. If the feeding rates indicated for higher densities of *Artemia* apply for biomass equivalents of much larger organisms, the large capacity of the mackerel suggests that relatively infrequent encounters with such organisms would sustain the daily requirement in an average sense. The present study and that of Kariya and Takahashi (1969) indicate that feeding can be expected to continue towards full capacity regardless of state of fullness when food becomes available.

Though mackerel may have to depend in part on larger organisms, it is possible that the food

potential of the larger crustaceans, and even very young fish, is greater than indicated by average area densities. The definite filtering response of the mackerel, which appears to be an adaptation for capturing the smaller organisms it utilizes at a greater rate than would be possible by biting activity when density is high, implies that high densities are a factor of some consequence in the feeding ecology of the species. One possible explanation is that the various kinds of food organisms tend to be distributed contagiously, with aggregations of considerably higher density than reflected by area averages. As Ivlev (1961) demonstrated with carp fry, feeding rate can be expected to increase with degree of aggregation for a fixed quantity of food organisms. Euphausiids have been observed in schools and breeding swarms (Brinton, 1962). More than likely the filtering response is evoked in mackerel with empty or near-empty stomachs by densities not much above the equivalent of 1 or 2 *Artemia*/liter, where rate of effective biting must already be on the order of 60 or more per minute. At 4 to 5 *Artemia*/liter the daily nutritional requirement could be obtained in less than 45 min of filter feeding.

Whereas *Artemia* adults represent the smallest organisms consumed by the mackerel, they represent the largest organisms commonly consumed by the anchovy (Loukashkin, 1970); the latter also consumes phytoplankton and crustaceans less than 1 mm in length by filter feeding. The wet weight quantities of *Artemia* adults consumed at different densities (Table 5), based on the present study for the mackerel and on Leong and O'Connell (1969) and O'Connell (1972) for the anchovy, suggest the differences in utilization and nutritional value of large crustaceans for equivalent age groups of the two species.

The anchovy requires far less food than the mackerel to meet its daily nutritional requirement, and can obtain the necessary quantity in about 20 min when *Artemia* adults are at densities of 1 or more per liter. In this same period the mackerel consumes more than the anchovy at all densities, but not enough to satisfy the daily requirement. When considered in terms of the weight of the two fish, the greater quan-

TABLE 5.—Comparison of *Artemia* adults consumed (mg wet weight) by the 1-year-old mackerel and anchovy for different density levels of *Artemia* in the water.¹

Item	Mackerel	Anchovy
Age in years	1+	1-
Weight \pm g	147	4
Nutritional requirement:		
Percent body weight	8	6.8
mg	11,784	270
Minutes of feeding for nutritional requirement at:		
1 <i>Artemia</i> /liter	97	20
5 <i>Artemia</i> /liter	35	20
Mg <i>Artemia</i> consumed in 20 min with <i>Artemia</i> at:		
0.1 <i>Artemia</i> /liter	240	~152
1 <i>Artemia</i> /liter	600	270
5 <i>Artemia</i> /liter	9,600	270
Mg <i>Artemia</i> consumed/g fish weight in 20 min with <i>Artemia</i> at:		
0.1 <i>Artemia</i> /liter	1.6	~38
1 <i>Artemia</i> /liter	17	68
5 <i>Artemia</i> /liter	65	68

¹ Calculations for the anchovy at age 1+ and weight 7 g show the nutritional requirement and amounts consumed in 20 min at 1 and 5 *Artemia*/liter to be 475 mg, but all other values are the same as for the 4-g anchovy.

tities consumed by the mackerel have a relatively lower nutritional value than those consumed by the anchovy, except, perhaps, at very high densities.

The extreme difference in quantities consumed by the two species at high densities is attributable to the filtering capability of the mackerel, and the failure of the anchovy to filter feed on the larger crustaceans, regardless of density. No meaning can be attached to the small difference at the lowest density level because calculation of the values involved considerable extrapolation. It is nevertheless probable that the anchovy tends to remove large crustaceans at a lower rate than the mackerel at such levels. O'Connell (1972) showed that the feeding activity of the anchovy is likely to be divided between these and the smaller crustaceans captured by filtering if the larger organisms are less than about 5 to 8% of the dry weight of total zooplankton concentration.

From the above considerations it is tentatively hypothesized that the individual mackerel generally utilizes a greater proportion of the large crustaceans in the sea than does the individual anchovy, but that the proportion utilized generally has a relatively low nutritional value for the mackerel.

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