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The Interrelation of Biting and Filtering in the Feeding Activity of the Northern Anchovy (*Engraulis mordax*)

CHARLES P. O'CONNELL

National Oceanic and Atmospheric Administration
National Marine Fisheries Service, Fishery-Oceanography Center
La Jolla, Calif. 92037, USA

O'CONNELL, C. P. 1972. The interrelation of biting and filtering in the feeding activity of the northern anchovy (*Engraulis mordax*). J. Fish. Res. Bd. Canada 29: 285–293.

A previous study showed that the northern anchovy (*Engraulis mordax*) captures *Artemia* adults (3.7 mm long) by biting and *Artemia* nauplii (0.65 mm long) by filter feeding. This study shows that the ratio of biting to filtering activity in small schools varies with the relative concentration of *Artemia* adults and nauplii in the water. Activity was half biting and half filter feeding when *Artemia* adults were 2% by dry weight of the available biomass, but was entirely biting when *Artemia* adults exceeded about 7% of the biomass.

It is estimated that when feeding activity is half biting and half filtering, *Artemia* adults and nauplii would contribute equal dry weights to ingestion, and that the sum of the two would be the same as that possible if total activity had been filtering. When relative concentration of *Artemia* adults is high enough to induce total biting activity, the dry weight ingested per unit time would be double that possible by filtering alone on the nauplii present.

Ratios of large-to-small crustaceans are relatively high near the surface at night off southern California, which suggests that biting activity could often exceed 50% of total feeding activity. If the plankton does support a high percentage of biting activity, a large part of the area should usually provide the anchovy with its daily nutritional needs.

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Une étude antérieure a démontré que les anchois (*Engraulis mordax*) capturent les *Artemia* adultes (3.7 mm) à coups de dents et qu'elles se nourrissent par filtration de nauplii d'*Artemia* (0.65 mm). La présente étude révèle que le rapport morsure–filtration dans les bancs de taille restreinte varie en fonction de l'abondance relative des *Artemia* adultes et des nauplii dans le milieu. L'alimentation se fait moitié par morsure, moitié par filtration, quand les *Artemia* adultes constituent 2% en poids sec de la biomasse disponible, mais entièrement par morsure quand les *Artemia* adultes dépassent environ 7% de la biomasse.

Nous estimons que lorsque l'alimentation se fait moitié par morsure, moitié par filtration, les quantités d'*Artemia* adultes ingérées sont les mêmes en poids sec que celles des nauplii, et que le total des deux équivaut au total possible par filtration seulement. Lorsque la concentration en *Artemia* est suffisante pour induire une activité entièrement de morsure, le poids sec ingéré par unité de temps serait deux fois plus grand que celui possible par filtration seulement des nauplii.

La proportion des gros crustacés par rapport aux petits est relativement élevée près de la surface, la nuit, au large de la Californie méridionale. La morsure constituerait donc plus de 50% de l'activité alimentaire totale. Si, en réalité, le plancton est l'objet d'un fort pourcentage de morsure, une grande partie de la région pourrait généralement répondre aux besoins alimentaires quotidiens de l'anchois.

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LEONG and O'Connell (1969) showed that the northern anchovy (*Engraulis mordax*) captured *Artemia* nauplii by filtering, but captured the much larger *Artemia* adults individually by directed biting (particulate feeding) when each food was presented separately. Food biomass was accumulated more rapidly by biting than by filtering. They hypothesized that the anchovy could not sustain its daily food requirement by filtering alone off southern California, except in limited areas of heavy plankton concentration. Their study suggested that the role of biting activity could not be satisfactorily appraised until the response of the fish to mixed size assemblages of food organisms was better understood.

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The ability of the anchovy to capture larger but less abundant organisms by biting in addition to capturing the more numerous small organisms by filtering could be advantageous for two reasons. First, larger crustaceans with good escape responses might avoid capture by filtration. The directed nature of biting probably overcomes the escape response. Second, a greater volume of water can be searched in biting than can be strained in filtering. Either of these factors could raise the average amount of food eaten above what it would be by filtering alone.

The two modes of feeding suggest that the anchovy is a selective feeder. A number of authors have suggested on the basis of field studies that clupeoid fishes feed selectively and that food-organism size is a major determinant. Hiatt (1951), for example, showed that the nehu (*Stolephorus purpureus*) was larger and tended to have more food in its stomach in areas where large crustaceans were more available, and appeared to select these organisms. Brooks and Dodson (1965) concluded that the alewife (*Alosa pseudoharengus*) tended to select the larger crustaceans. Shen (1969) showed that zooplankters were generally more numerous than phytoplankters in the stomachs of *Engraulis japonicus*, and that the larger organisms, up to 5 mm long (Euphausiacea, Ostracoda, *Paracalanus*, and Rotifera), were commonly present in the stomachs, though only occasionally in relatively high abundance. Loukashkin (1970) showed that zooplankters were usually far more abundant than phytoplankters in the stomachs of *E. mordax*, and concluded that large copepods and euphausiids were the most important food items.

These studies imply that larger crustaceans are taken in preference to smaller organisms as their relative abundance permits. They suggest the hypothesis that ingestion rate will vary in respect to biomass concentration of plankton as the proportion of biting to filtering activity varies in some way with the relative abundance of large and small organisms in the concentration. This study attempts to describe the way in which these two kinds of feeding activity are used by small schools of anchovies in the laboratory when they are presented with different density combinations of *Artemia* adults and nauplii. The implications of these results are discussed in relation to anchovy feeding in the sea.

Procedure

Feeding trials were carried out in an arrangement of two plastic pools with connecting trough and gates (Leong and O'Connell 1969). The pools were supplied with a continuous flow of filtered sea water and each contained 3.65 m^3 of water at a depth of 0.5 m. The pools were under a 12-hr day–12-hr night cycle of illumination, but all trials were during the day. Temperature ranged from 16 to 19 C.

For each trial, water flow was turned off and 16–20 fish were diverted from a large reserve school in one pool to the trough and then admitted to a prepared food situation in the other pool. Three observers scored feeding activity for a period of 8 min, after which the fish were returned to the reserve school. All trials were preceded by at least 24 hr without feeding and samples from the reserve school always showed empty digestive tracts.

The food situation was established for each trial by placing a known number of *Artemia* adults averaging 3.7 mm long (0.5 mg dry wt) and an approximately known number of Artemia nauplii averaging 0.65 mm long (0.00145 mg dry wt) in the experimental pool and dispersing them by stirring gently with wide mesh dipnets. *Artemia* adults were precounted for all but a few high density trials, for which they were estimated by wet weight. Post-trial estimates of nauplii density were made from samples taken from the pool just before the fish were admitted.

The basic units of observation over the 8-min feeding period were 10-sec intervals marked by an audible timing device. Each of the three observers recorded the activity of a single fish as biting (B), filtering (F), or none (0) for successive intervals. The two kinds of activity, which differ by a factor of at least 10 in duration of mouth opening (Leong and O'Connell 1969), were easily distinguished. Instances of one fish displaying both kinds of activity in the same 10-sec interval were rare. Prior to each trial, each observer was assigned a different part of the school — front, middle, or rear — and chose fish in these approximate positions at the start of each interval. Observer differences will be considered in conjunction with the analysis of position differences in activity.

A pilot study indicated that the proportion of biting to filtering activity in the school might vary in relation to the relative concentration of the two sizes of *Artemia* in the water, only when *Artemia* adults were at fractions of less than about 10% of the dry weight of total food concentration. Feeding activity appeared to be directed almost entirely at larger organisms when they constituted greater fractions than this of the available food. Groups of six fish allowed to feed for 5 min averaged 56% of adult *Artemia* in dry weight of digestive tract contents, when these larger organisms were 5% or less by dry weight of the food in the water (four trials), but averaged 95% or more adults in digestive tract contents when adults were between 7 and 99% of the food in the water. The experiment was therefore limited to density combinations in which *Artemia* adults were a small fraction of the total dry weight of available food. The fractions varied from 0.4 to 11% of total dry weight, with over half of the trials having 3% or less and another one-third having between 3 and 7%. The density ranges of each food type were extended as far as practicable within this limitation.

The pilot study also suggested that a behavioral measurement would probably be a more reliable indicator of the response to the food situation existing at the start of each trial than would digestive tract contents. Though both activities were evident in the trials that showed approximately equal dry weight fractions of the two food types in digestive tracts, and biting was distinctly dominant in the other trials, activity did appear to shift towards less biting and more filtering in the last few minutes in a few cases. Such change probably signified elimination of all or most of the larger organisms as feeding progressed.

Effect of *Artemia* Adult and Nauplii Densities on the Proportion of Biting to Filtering Activity

The response of the school to food concentrations in which *Artemia* adults were a small fraction of total dry weight at the start of the trial is described from the feeding activity occurring in the first 3 min of 46 trials. Though response was measured for 8 min, biting activity tended to be constant and maximal only during the first 3, as indicated by activity averaged for all trials (front bars in Fig. 1). Filtering activity was not maximal in the first 3 min, but rather started low and increased steadily over the feeding period. Schools exposed to nauplii alone (rear bars in Fig. 1) showed the same kind of steady increase in filtering activity.

Though interpretation of the first minute is uncertain, the response patterns in general suggest that where *Artemia* adults are present along with nauplii, biting tends to replace filtering rather than be in addition to it.

Figures 2 and 3 show the relation of biting and filtering activity in the first 3 min of feeding to the starting densities of *Artemia* adults and nauplii. Biting tended to increase with adult density and filtering tended to increase with nauplii density, but in each case the relation of response to density appeared to be lower where densities of the alternative food were higher. This suggests that the school shows a ratio of biting to filtering activity that varies with the densities of both groups of *Artemia*.

Table 1 indicates the effect of each type of food on the relative amounts of biting and filtering, which was calculated as percent biting (the ratio of 10-sec time units scored as biting to the total scored as biting and filtering in the first 3 min). The table is based on the 24 trials with *Artemia* adults between 4 and $50/m^3$ and *Artemia* nauplii between 100,000 and $500{,}000/m^3$. The distribution of these trials permitted separation into four equal groups representing low and high density treatments of comparable range for each food factor. The food density means and ranges are given along with the average percent biting response for each of the food treatment combinations. Percent biting increased with *Artemia* adult density at both levels of nauplii density and decreased

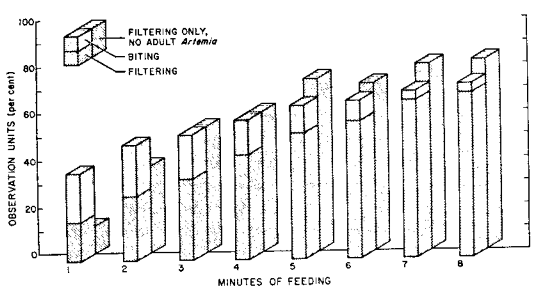

FIG. 1. Percentages of filtering and biting activity for each minute of the trial period. Front bars represent averages by minute for 42 trials in which fish were exposed to combinations of *Artemia* adults and nauplii. Rear bars represent averages by minute for 6 trials in which fish were exposed to nauplii alone. Average nauplii density was higher for the latter series of trials.

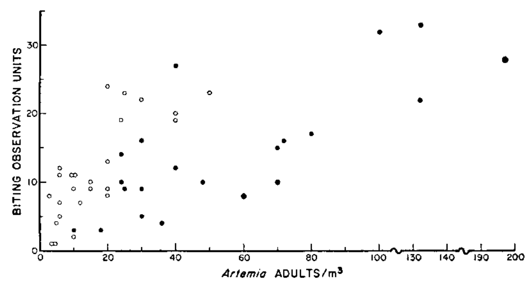

FIG. 2. The relation of biting observations to density of *Artemia* adults for 46 trials in which both adults and nauplii were present. Density of *Artemia* nauplii: ○, < $400{,}000/m^3$; ●, > $400{,}000/m^3$.

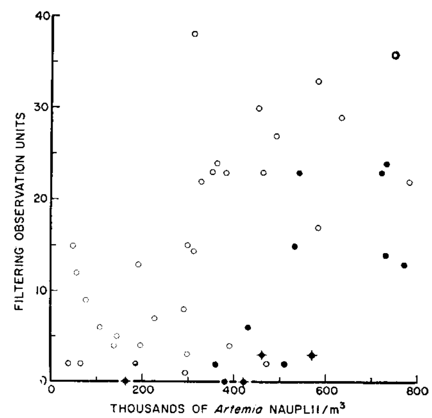

FIG. 3. The relation of filtering observations to density of *Artemia* nauplii for 46 trials in which both adults and nauplii were present. Density of *Artemia* adults: ○, < $40/m^3$; ●, > $40/m^3$; -+-, > $100/m^3$.

with nauplii density at both levels of adult density. An analysis of variance showed that only the two main effects were important, and that percent biting was largely associated with the density of *Artemia* adults ($F = 11.0$, df 1/20), but nauplii did have a discernible effect ($F = 1.58$, df 1/20), which would probably have been stronger if the average density of *Artemia* adults had been more nearly alike for the two treatment combinations in which adults were high. In any event, percent biting will be described as a function of *Artemia* adult density for broad ranges of nauplii density.

Trends of relative biting and filtering are shown by normal probability plots of percent biting (PB) on *Artemia* adult density for three different ranges of nauplii density (Fig. 4). Probit analysis was used to estimate the parameters of the fitted lines for suitably limited ranges, i.e., for values excluding 0 and 100% response. Individual points represent PB values for trials pooled in successive intervals of four *Artemia* adults/m^3. Trials with nauplii densities below 100,000/m^3 were excluded because they encompassed too narrow a range of *Artemia* adult density, and trials with adult densities above 100/m^3 were excluded because a few would have produced responses of 100%, a nonexistent value on the probit scale.

The data for the highest range of nauplii density were judged to be inconclusive because the PB values obviously did not show a significant trend. The only distinguishable increase in response was the PB value for the highest *Artemia* adult density. The arrays for the other two ranges, however, do show good evidence of linear trends, and regressions for each can therefore be taken to represent cumulative normal distributions (Bliss 1967) with parameters $\hat{\mu}$ and σ, where $\hat{\mu}$ is the mean density of adults at 50% response and $\hat{\sigma}$ is the standard deviation. Values for these parameters are given in Table 2. The χ^2 values show that the array of PB values for the lowest

TABLE 1. Average percent biting for four treatment combinations of *Artemia* adult and nauplii density. Mean density and range of adults (A) and thousands of nauplii (N) is shown for each treatment combination.

Artemia adult density	*Artemia* nauplii density: Low	*Artemia* nauplii density: High
Low	42	24
	A 10(*4–15*)	11(*6–18*)
	N 242(*107–311*)	389(*325–465*)
High	79	69
	A 27(*20–40*)	35(*20–50*)
	N 219(*141–298*)	416(*360–484*)

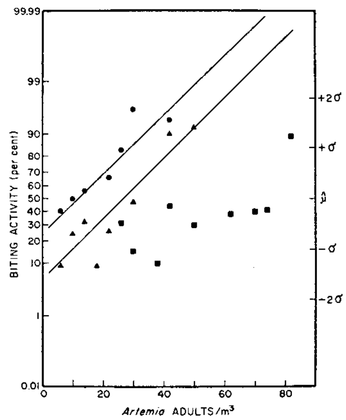

FIG. 4. Probit regressions of percent biting response on density of *Artemia* adults for three categories of *Artemia* nauplii density. *Artemia* nauplii density: ●, 100–300 thousand/m^3; ▲, 300–500 thousand/m^3; ■, > 500 thousand/m^3. Mean and standard deviation of response are indicated at right.

TABLE 2. The normal cumulative distributions that describe the relation of percentage biting response to density of *Artemia* adults for three categories of *Artemia* nauplii density. $\hat{\mu}$ is mean and $\hat{\sigma}$ is standard deviation of the distributions. *n* is the number of 10-sec response units and N is the number of *Artemia* adult density classes in which they occurred. Significant χ^2 values indicate departure from normality.

Nauplii density range '000/m^3	*n*	N	μ	$\hat{\sigma}$	χ^2
100–300	214	7	11.78±2.78	17.10±3.44	4.08
300–500	342	8	26.70±1.34	17.00±1.76	16.21[a]
500+	381	9	–	–	27.58[b]

[a]$P = 0.05$.
[b]$P = 0.01$.

range of nauplii density is acceptably normal, while that for the high range is not, and that for the middle range is uncertain. In view of the graphic evidence, the deviation from normality indicated for the middle range is probably attributable to inflation of variability, a not unexpected result where the experiment occurred over a long time and the results from individual trials were combined irrespective of the time element for analysis. Use of the uncorrected estimates of $\hat{\mu}$ and $\hat{\sigma}$ means only that the standard errors for each should be considered conservative.

The regression lines for the low and middle ranges of nauplii density, which have the same slope (0.59), and which represent normal cumulative functions that differ only in mean ($\hat{\mu}$), show that the proportion of feeding activity devoted to biting rather than filtering by small schools of anchovies increased as density of *Artemia* adults increased, and/or as density of nauplii decreased. The expected percent of biting activity can be estimated directly from Fig. 4 for any density of *Artemia* adults with *Artemia* nauplii assumed to be at a density of 200,000/m^3 or 400,000/m^3.

The above distributions define percent biting as an average for the school, but the average is based on summation over three positions in the school, and analysis by position indicates that there is a gradation of feeding response within the school. To evaluate the significance of position differences, however, it is necessary to test the hypothesis that variation in feeding activity with position is not associated with variation between observers. Since the positions were not occupied an equal number of times by each observer among all trials, the hypothesis was tested for 24 trials in which each observer was at each position eight times. The numbers of 10-sec intervals scored as biting (B), filtering (F), and zero (0) activity over the first 3 min is shown in Table 3 by position for all of these trials, and by observer for each position. Feeding activity differs markedly between positions (χ^2 = 74.6), with biting higher than filtering at the front and filtering higher than biting at the middle and rear. Though not grouped as such in the table, differences between position for each observer show the same marked pattern. χ^2 values are 43, 44, and 52 (df = 4) for observers A, B, and C, respectively.

The χ^2 values for the three positions, as given in the table, show, on the other hand, that all three observers scored essentially the same distribution of biting, filtering, and zero observations for the front and rear positions. There is significant deviation from expected at the middle position, although all three observers did score more filtering than biting. Inequities in the average food situation represented by the eight trials for each observer were greater at the middle than at the front and rear positions, and may have been partly responsible for the higher deviations in this set. Variation at the middle position notwithstanding, it can be concluded from these tests that differences between positions are far greater than differences between observers.

The nature of the gradient in feeding activity is evident in probit regressions for each of the three school positions — front, middle, and rear — for

TABLE 3. Contingency tables and χ^2 values for relation of the number of 10-sec intervals scored as biting (B), filtering (F), and zero (0) feeding activity in 3 min to position of observation in the school, and to observer at each position. n = number of feeding trials in which each position was observed. df = degrees of freedom. Expected distributions are shown in parentheses.

Position	Observer	n	B	F	0	χ^2	df
Front	All	24	132	51	249	74.6***	4
Middle	All	24	59	174	199		
Rear	All	24	74	137	221		
			(88.3)	(120.7)	(223.0)		
Front	A	8	51	19	74	8.32	4
	B	8	42	10	92		
	C	8	39	22	83		
			(44.0)	(17.0)	(83.0)		
Middle	A	8	29	56	59	19.3***	4
	B	8	18	45	81		
	C	8	12	73	59		
			(19.7)	(58.0)	(66.3)		
Rear	A	8	28	50	66	7.14	4
	B	8	20	52	72		
	C	8	26	35	83		
			(24.7)	(45.7)	(73.7)		

trials in the 100,000–300,000 nauplii/m³ range (Fig. 5A) and for trials in the 300,000–500,000 nauplii/m³ range (Fig. 5B). The regressions were fitted to PB values calculated for each position for the same combinations of *Artemia* adult and nauplii densities for which the average PB values were calculated. For the lower nauplii range (Fig. 5A) no regression was calculated for the front position because five of the PB values were 100%. These and the two values shown for the front position, nevertheless, demonstrate that fish in the lead position consistently showed far higher percentages of biting than fish in following positions. For the higher range of nauplii density (Fig. 5B) the same phenomenon is evident but less pronounced. Here, however, the line for the middle position indicates that percent biting response became as strong in the middle as in the front position when *Artemia* adult density was high. The general pattern is clearly a gradation from higher percent biting at the front to lower percent biting at the rear with variations in the strength and intensity of gradient dependent on the relative abundance of the two sizes of organism in the water.

Contributions of Biting and Filtering to Ingestion Rate

Average ingestion rate for individuals in the school, and the contribution of *Artemia* adults and nauplii to this average, must depend on the rates at which the two sizes of organism are captured as well as on the ratios for the two associated feeding activities in the school. The relation of numbers captured to density for nauplii is suggested by equation 5 in Leong and O'Connell (1969). Those authors also described feeding rate for *Artemia* adults, but only for densities above 1000/m³. Feeding rate for low densities of adults can be estimated for simulated daylight conditions from the pilot study described under methods above. In 10 of the trials nauplii were essentially ignored by the fish, and the relation between *Artemia* adults in the water and in digestive tracts was

No./m³	6	6	8	8	12	18	100	100	1000	10,000
No./fish	1	1.5	2	3	4.7	8.3	19	25	95	78

The correlation is obvious, except that average number consumed was no higher for a density of 10,000/m³ than for a density of 1000/m³. This is consistent with the finding by Leong and O'Connell (1969) that number of *Artemia* adults consumed by the anchovy was not related to density over the range 1000/m³–25,000/m³. If the 10,000/m³ entry is excluded on the assumption that it is far above some inflexion point where feeding rate ceases to increase with density, the relation for the remaining nine pairs of values ($r = 0.97$) is described by the line

$$\text{Log } N = 0.82 \text{ Log } D - 0.36 \qquad (1)$$

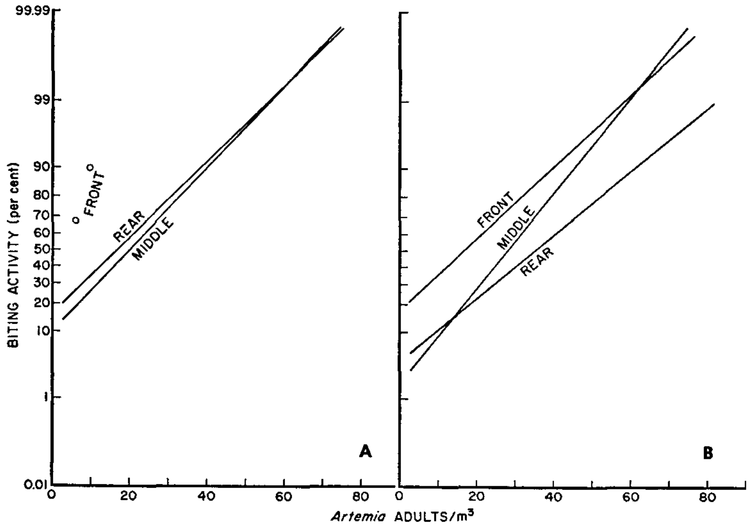

FIG. 5. Probit regressions of percent biting response on density of *Artemia* adults for front, middle, and rear positions in the school for trials with A, *Artemia* nauplii in the 100–300 thousand/m³ range, (No regression line is shown for the front position because 5 of the 7 points were off scale at 100%), and B, *Artemia* nauplii in the 300–500 thousand/m³ range.

where N = average number of *Artemia* adults consumed in 5 min, and D = average number of *Artemia* adults/m³ present in the water at the start of feeding.

Under the assumption that basic rates derived from equation 1 above and equation 5 in Leong and O'Connell (1969) are effective in proportion to the ratios for the two kinds of feeding activity in the school, the products of these basic rates and ratio values for the densities present should provide a partial rate for each size of organism. The sum of the partial rates, expressed in comparable units, will be the average total rate for the density combination. Basic, partial, and total rates are shown for four density combinations in Table 4. The rates are expressed as the milligram dry weight that would be consumed in 1 min by a fish weighing 5 g (average weight of fish in pilot study). The four density combinations are based on the midpoints of the nauplii density ranges for which probit regressions were calculated and on the adult densities indicated by those regressions (Fig. 4) for 50 and 99% biting activity.

The values in Table 4 indicate that when dry weight concentration of *Artemia* adults in the water is 2% of the total concentration, the basic rates are similar for the two sizes of organism and particulate and filter feeding activity are equal. Under these circumstances the ingestion rate for both sizes together, or total rate, is no greater than would be possible by filtration alone on the nauplii. However, when the dry weight concentration of *Artemia* adults is in the order of 5.5–8% of the dry weight of adults and nauplii together, the basic rate for *Artemia* adults is approximately double that for nauplii. Under these circumstances total ingestion rate is approximately double that possible by filtration alone, and filter feeding contributes little to total ingestion.

The possibilities of ingestion rate, of course, are not limited to the combinations illustrated. Total ingestion rate would presumably be intermediate between those for 50 and 99% biting activity if density of larger organisms were intermediate between those that support such levels of biting. Ingestion rate might also be more than double the filtration potential if the density of larger organisms were markedly greater than necessary for the 99% level of biting activity. Also, ingestion rates might be somewhat lower, or the concentrations of large organisms necessary to sustain them somewhat higher than indicated, if escapement of larger crustaceans in the sea is appreciable. Though biting may tend to counteract escapement, the calculations are based on *Artemia* adults, which appear to have no effective escape response.

Interrelation of Biting and Filtering in the Sea

Although the anchovy probably relies on filter feeding for a steady supply of food in the sea, this supply may often fail to sustain the daily nutritional requirement, as already hypothesized. The experiments described here suggest that biting could be an augmenting activity of some consequence, depending on the size composition of the plankton. O'Connell (1971) showed that plankton pump samples from surface waters off southern California vary greatly in relative abundance of large and small crustaceans. Of the constituents described, small copepods, with an average dry weight equivalent of 0.0025 mg, and euphausiids, with average dry weight equivalents of 0.042 mg for day samples and 0.293 mg for night samples, most closely approximate the *Artemia* nauplii and adults used in the laboratory

TABLE 4. Estimated ingestion rates for density combinations of *Artemia* adults and nauplii at which biting activity is 50 and 99% of total feeding activity.

	Low nauplii density				High nauplii density			
Percent biting activity	50		99		50		99	
Organism type	Nauplii	Adults	Nauplii	Adults	Nauplii	Adults	Nauplii	Adult
Density no./m³	200,000	12	200,000	52	400,000	27	400,000	66
Dry wt mg/m³	290	6	290	26	580	13.5	580	33
Adult % of total dry wt		2.0		8.2		2.3		5.4
Ingestion rates (mg dry wt/min) for above densities								
Basic	0.49	0.34	0.49	1.1	0.73	0.65	0.73	1.4
Partial	0.24	0.17	0.01	1.1	0.37	0.33	0.01	1.4
Total		0.41		1.1		0.70		1.4

study. They also constituted the bulk of the dry weight of the samples. Averages for five cruises indicated that euphausiids were 3–5% of the dry weight of both groups during the day and 21–66% at night. These percentages suggest that anchovy feeding in surface waters would be chiefly filtering in the daytime and chiefly biting at night, with ingestion rate far exceeding the filtration potential in the latter period.

However, the small laboratory school can scarcely represent more than the leading edge of many schools in the sea. Since percentage of biting diminished noticeably in following positions in a small school, it is possible that diminution extends to a complete lack of opportunity for biting activity for most of the fish in large, compact schools. This would result in a lower capture rate of the larger crustaceans and a lesser elevation of total digestion rate, on the average, than might be expected for a small school exposed to the same relative concentrations.

There is circumstantial evidence to suggest, on the other hand, that the anchovy schools more loosely when larger food organisms are abundantly available. In the laboratory experiments the fish schooled under all trial circumstances, but in the presence of the higher densities of *Artemia* adults, where initial activity was largely biting, they appeared to swim faster and be more widely separated than in circumstances where most of the activity was filtering. Hobson (1968), on the basis of extensive field observations, found that the flatiron herring, *Harengula thrissina*, remained inshore in dense schools during the day and moved offshore, possibly in looser aggregations, to feed at night when shrimp-like crustaceans were most abundant in midwaters. He cited other clupeids that have been observed to break up into smaller, more loosely associated feeding groups at night. Such a behavior pattern, which might well apply to the northern anchovy, would operate to improve the average rate of encounter with larger crustaceans, and thereby raise the average rate of ingestion in respect to the filtration potential, although perhaps still not as much as might be expected for a small laboratory school.

Whatever the daily feeding cycle of the anchovy, it appears that opportunities for biting activity would be greatest in dim light — either at depth during the day, or near the surface at night. Because of strong vertical migration, high densities of euphausiids are common only under these conditions, and O'Connell (1971) has shown that the larger copepods, which may also elicit biting, have a vertical migration pattern similar to that of the euphausiids. Small copepods, on the other hand, showed evidence of only a slight nighttime increase at the surface.

Feeding by biting, because it is so obviously dependent on visual perception of individual organisms, may not seem compatible with low nighttime levels of illumination, but there is some evidence to the contrary. Hobson (1968) commented that some authors greatly underestimate the extent to which vision can be used at night by both predators and prey. Hunter (1968) showed that juvenile jack mackerel (*Trachurus symmetricus*) obtained 50% of the usual daytime ration when feeding by biting on *Artemia* adults at a light intensity as low as would occur near the surface on a full moonlit night. He noted, also, that more visible energy may exist in the sea than his calculations indicate. Blaxter (1964) listed a number of "visual" feeders that stopped feeding at similarly low light intensities. In regard to the northern anchovy, O'Connell (1963) showed on anatomical grounds that this species has a retina that is probably better adapted

TABLE 5. Hours of feeding necessary for an anchovy weighing 5 g to obtain its daily nutritional requirement (74 mg dry wt) from observed nighttime plankton concentrations for four different percentages of particulate feeding activity. Rules separate the values at 12 and 24 hr.

Zooplankton concentration mg/m³ dry wt	% samples	Hr of feeding: Filtering only	50% biting	75% biting	99% biting
10	27	84	84	56	42
20	17	42	42	28	21
30	41	28	28	19	14
40	10	21	21	14	11
50	5	17	17	11	9

than that of the jack mackerel for dim-light vision.

From all of the above evidence it seems highly probable that the anchovy can feed by biting at night, and by so doing effectively exceed the limitations of filtering. Loukashkin's (1970) finding that euphausiids and large copepods were the most important items in stomach contents of the anchovy tends to confirm this view.

Leong and O'Connell (1969) evaluated the food potential of zooplankton concentrations in the sea for the anchovy by estimating the hours of filtering necessary to obtain the daily nutritional requirement. Table 5 suggests the way in which different percentages of biting activity might effect this index of food potential, where the different percentages of biting imply that a given concentration is composed of different though undefined proportions of large and small organisms. The percentage distribution for dry weight concentrations is based on the night samples from five plankton pump cruises (O'Connell 1971). Hours of filtering for each dry weight class were calculated on the assumptions that a 5 g anchovy requires 74 mg dry weight of food per day and filters water at the rate of 1.46 liters/minute (Leong and O'Connell 1969). Hours of feeding for percentages of biting were calculated on the basis of the relations suggested in Table 5. That is, ingestion rate is no different for plankton that elicits 50% biting than for plankton that elicits filtering only, but varies proportionately from a factor of one at 50% biting to a factor of two at 99% biting. Feeding duration is inversely proportional to feeding rate.

The calculated values, which are separated by lines at 12 and 24 hr in the table, indicate that with low biting activity only 15% of the area sampled would have provided the anchovy with its nutritional requirement in one day. The same fraction of the area would have provided the daily requirement in less than 12 hr if the plankton concentrations supported relatively high average percentages of biting. If feeding extended over more than 12 hr with a high percentage of biting most of the time, more than half of the area could have provided the required nutrition. The anchovy may capture large organisms less effectively in relation to density at night than indicated earlier for simulated daylight conditions, but given the high ratios of euphausiid to small copepod dry weight in night samples, some average percentage of biting well above 50% seems entirely possible. Availability of the daily nutritional requirement would also tend to be widened if the anchovy utilizes phytoplankton along with zooplankton. These considerations suggest that plankton is usually adequate for the nutritional needs of the anchovy in a large part of the surface waters off southern California.

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