

THRESHOLDS FOR FILTER FEEDING IN NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

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ABSTRACT

The density threshold for the onset of filter feeding in adult anchovy (*Engraulis mordax*) fell between 5 and 18 *Artemia salina* nauplii/l, between 1 and 2 anchovy eggs/l, and between 151 and 328 *Gymnodinium splendens* cells/l. Observations of the incidence of filtering schools indicate that behavioral changes occurred at lower food densities. These observations also indicate that the intensity of filtering by anchovy schools may be a function of the biomass of filterable foods. Filtering persisted long after the density in the tank was reduced below that required for the initiation of filter feeding.

RESUMEN

La densidad mínima para el comienzo de alimentación por filtrado en adultos de *Engraulis mordax* disminuyó entre 5 y 18 nauplios de *Artemia salina* por litro, entre 1 y 2 huevos de anchoveta por litro, y entre 151 y 328 células de *Gymnodinium splendens* por litro. Observaciones sobre la incidencia de cardúmenes en proceso de actividad filtradora indican que se producen cambios en su comportamiento cuando el alimento aparece en densidades bajas. Estas observaciones también indican que la intensidad de filtrado en los cardúmenes de anchoveta puede estar determinada por la biomasa de alimento filtrable. Este tipo de alimentación aún persistió mucho después de que disminuyera la densidad en el tanque, alcanzando valores por debajo del umbral que marca el comienzo del proceso de alimentación por filtrado.

INTRODUCTION

Northern anchovy are facultative filter-feeding planktivores. They change from filter feeding to particulate feeding on the basis of prey size; they filter small prey, such as *Artemia salina* nauplii, and bite larger ones, such as *Artemia* adults (Leong and O'Connell 1969). A significant proportion of the natural mortality of northern anchovy eggs can be attributed to adult anchovy filtering their eggs (Hunter and Kimbrell 1980; MacCall 1980), but the extent to which eggs are filtered selectively or taken inadvertently while filtering other prey is not known. Selec-

tive filtering requires that the density of prey be sufficient to cause the school to filter intensively within an aggregation of a particular prey. Thus, the prey density thresholds for filter feeding are important in modeling effects of egg cannibalism as well as in understanding the ecology of anchovy feeding. The densities of prey used by Leong and O'Connell (1969) to estimate maximum filtering rates of anchovy (292-1,120 *Artemia* nauplii/l) are far above the threshold. The objective of this study was to estimate the prey density threshold for filtering in northern anchovy. Three prey types are used: *Artemia* nauplii (0.433 mm x 0.236 mm; 1.70 μ g dry weight); northern anchovy eggs (1.34 mm x 0.66 mm; 30.1 μ g dry weight); and the dinoflagellate *Gymnodinium splendens* (40 μ m dia; 0.0117 μ g dry weight).

METHODS

Schools of 56-596 northern anchovy (6.4-10.2 cm standard length) were maintained in a tank (3-m dia.; water depth 0.6 m) with continuous flowing seawater of ambient temperature (14.3-21.6°C). Seawater was filtered continuously through a sand-and-gravel filter and subsequently was irradiated with ultraviolet light. The tank was dimly lit from above by a 40-W incandescent lamp for 12 h per day and was dark for 12 h. Fish were fed trout food (Oregon Moist Pellets)¹ and frozen adult *Artemia salina* (brine shrimp). Schools were deprived of food for 48 h prior to an experiment, and a few hours before a test the tank was cleaned and the seawater shut off. Numbers of anchovy in schools varied (Table 1), and the tank was completely restocked 11 times over the 2 years that experiments were conducted. Partial restocking and some mortality account for the variability in school size.

At the onset of an experiment the tank was stirred vigorously with a large dip net (60-cm dia); the school recovered from this disturbance in 1-2 min. Immediately after stirring, the incidence of filtering behavior was recorded for 9 min. Food was then added and the tank stirred again while water samples were taken to estimate the density of food in the tank. After the tank was stirred for the second time, behavior ob-

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¹Use of a trade name does not imply endorsement by the National Marine Fisheries Service.

TABLE 1
 Effect of Prey Density and Prey Type on Filter Feeding in Northern Anchovy, *Engraulis mordax*, Schools

Food type		Significance of density change ²	Incidence of filter feeding		Significance of change ⁴	School Size n
Initial density n/l	Final ¹ density n/l		Before food added ³	After food added ³		
<i>Artemia</i> nauplii						
0.87	0.76	0	0	1.2	0	430
2.81	2.84	0	7.6	7.9	0	430
3.27	2.22	0	0.6	4.3	+	357
4.59	4.46	0	2.0	3.9	0	300
5.51	2.59	+	14.5	43.7	+	318
5.96	1.68	+	3.3	12.0	+	256
6.71	4.33	0	1.2	7.0	0	300
8.77	8.47	0	0.2	20.0	+	567
9.03	4.60	0	1.6	10.4	+	567
9.13	6.90	0	0.1	0.3	0	357
13.10	11.40	0	1.6	5.4	+	357
13.62	9.62	+	2.1	26.8	+	318
16.05	10.14	0	0	25.5	+	357
18.04	8.74	+	12.6	36.1	+	430
18.79	10.71	+	3.6	49.7	+	300
20.46	9.44	+	2.1	57.4	+	430
23.96	9.17	+	8.6	47.5	+	430
26.64	12.85	+	10.8	70.7	+	430
114	—	—	—	57.8	—	438
190	—	—	—	53.4	—	569
285	—	—	—	86.0	—	596
378	—	—	—	71.9	—	167
386	—	—	—	81.8	—	374
<i>Anchovy</i> eggs						
0.26	0.15	0	3.9	20.5	+	106
0.32	0.37	0	0.2	7.6	+	75
1.11	1.52	0	1.8	22.7	+	300
1.50	0.46	+	4.1	59.5	+	116
3.32	1.70	+	2.1	45.8	+	131
4.14	1.21	+	5.0	63.2	+	357
4.76	0.84	+	3.9	80.1	+	300
5.34	0.73	+	5.1	58.6	+	256
10.50	2.90	+	1.6	79.8	+	126
<i>Gymnodinium</i> cells						
151	104	+	0.2	7.8	+	—
161	104	0	2.1	31.2	+	—
259	200	+	0.4	9.3	+	56
328	358	0	0.6	3.2	+	67

¹Measured 9 min after food introduction in *Artemia* and egg experiments, and after 18 min in *Gymnodinium* experiments; five highest *Artemia* densities were preliminary experiments, and no final density was recorded.

²Comparison of initial and final density using t-test; + = $P < 0.05$ and 0 = $P > 0.05$ (2 tail).

³Average for 9-min test period.

⁴Comparison of mean incidence of filtering before and after food added using t-test when + = $P < 0.05$ and 0 = $P < 0.05$ (2 tail).

servations were resumed for 9 min, then the tank was stirred for the third time while another set of water samples was taken. In the *Gymnodinium* experiments the final set of water samples was not taken until 18 min after the introduction of food, in order to increase the probability of detecting a change in food density, since the filtering response was weak even at the highest density.

Methods for estimating food density in the tank varied. When the density was about four prey per liter or less we took seven 12-liter samples; at higher densities we took 12-15 one-liter samples. Water in each sample was filtered, prey were counted, and a mean

density was calculated. The t-test (2 tail) was used to compare initial to final food densities.

Filtering behavior was recorded by three to five observers stationed around the tank. Each observer watched a single anchovy for 2 sec. If the operculum was fully extended during any part of the 2-sec period, the observer recorded a filtering act. After recording on push-button counters whether or not a filtering act had occurred, the observer randomly selected another fish and continued to accumulate 2-sec observations of individual fish over a 2-min period. After 2 min each observer had accumulated a set of about 60 observations of 60 fish; the proportion of these observations in

which filtering occurred was transcribed and another 2-min observation period begun. In the 9-min test period, each observer made four sets of cumulative observations, and the number of sets per test period ranged from 12 to 20, depending on the number of observers. Each set was considered as an estimate of the incidence of filtering behavior in the school. The sets taken by all observers during a test period were combined, and a mean and variance were estimated assuming each set to be an independent observation. We used the t-test (2 tail) to determine if sets of observations taken before and after the addition of food differed from each other.

RESULTS

The density threshold for the onset of filtering of *Artemia* nauplii fell between 5 and 18 nauplii/l when a significant difference ($P < 0.05$) between initial and final density was the criterion (Table 1). No significant changes occurred at densities less than 5 nauplii/l, and initial and final densities were consistently different above 17 nauplii/l. Significant changes in the density of anchovy eggs occurred consistently at densities greater than two eggs/l, indicating that the threshold for the onset of filtering may occur between 1 and 2 eggs/l. The density of *Gymnodinium* changed significantly in two of the four experiments, indicating that a 50 percent threshold for filtering this dinoflagellate may fall between 151 and 328 cells/l.

Even when no food has been present for some time, usually a few fish, typically about 2 percent, execute

filtering movements. The frequency of such acts is low and their duration short: they may serve in early detection of food or may have some other function. At high food densities, similar to those used by Leong and O'Connell (1969), nearly all fish in a school filter, and filtering bouts are nearly continuous. At such densities, about 70-80 percent of the fish filter during any 2-sec period. At lower food densities, the frequency of filtering bouts and their duration decreases, and the time between bouts increases until, at the lowest densities, the behavior approaches that of fish without food.

The percentage of fish filtering usually increased when food was added, even at the lowest densities. Thus, significant changes in filtering behavior occurred at lower densities than those at which we were able to detect a change in food concentration caused by filtering (Table 1). The proportion of fish filtering increased with the initial food density but differed among food types (Figure 1). For a given density, the incidence of filtering was highest for anchovy eggs and intermediate for *Artemia* nauplii; only a small portion of the fish filtered *Gymnodinium* at densities as high as 328 cells/l. A strong response (filtering fish > 50 percent) occurred at food densities of 4 eggs/l and 20 *Artemia* nauplii/l; above these densities the incidence of filtering increased gradually with food density, reaching a maximum of about 80 percent.

The behavior data shown in Figure 1 were combined by expressing the initial food density in terms of dry weight per liter instead of numbers per liter. Con-

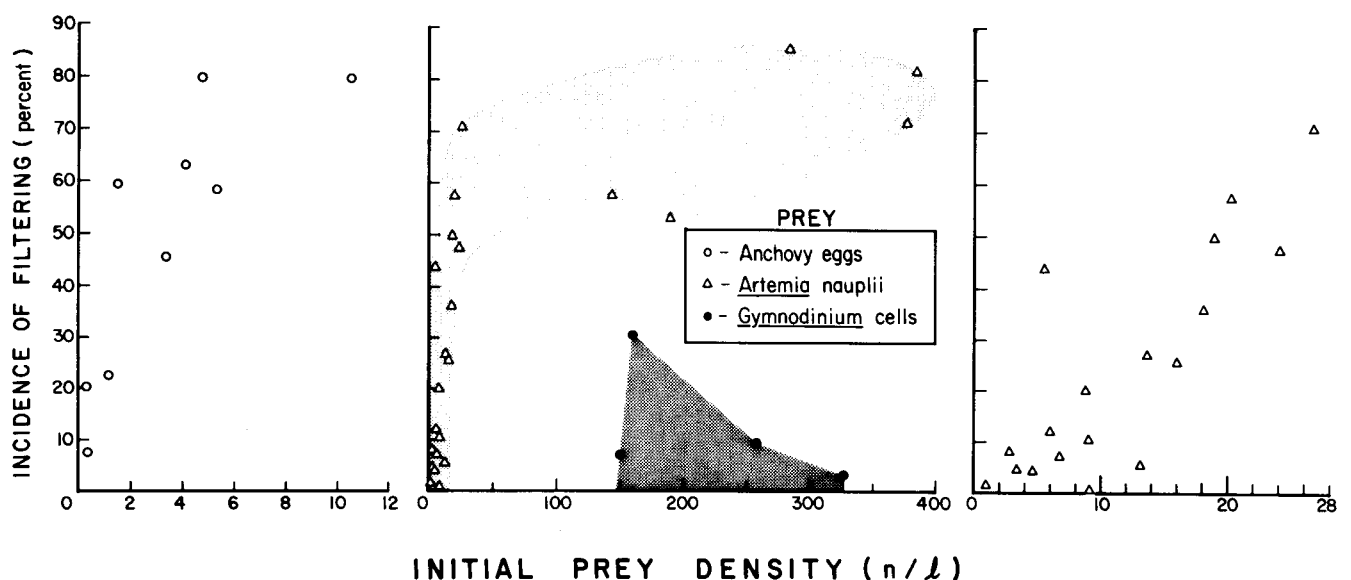


Figure 1. Mean incidence of filter feeding in northern anchovy schools during initial 9 min of feeding as a function of initial prey density in numbers per liter. *Left*, filtering incidence as a function of anchovy egg density; *center*, filtering incidence as a function of density of *Artemia* nauplii (lightly shaded) and *Gymnodinium* cells (darkly shaded); *right*, enlargement of *Artemia* nauplii data for densities of 1-27/l.

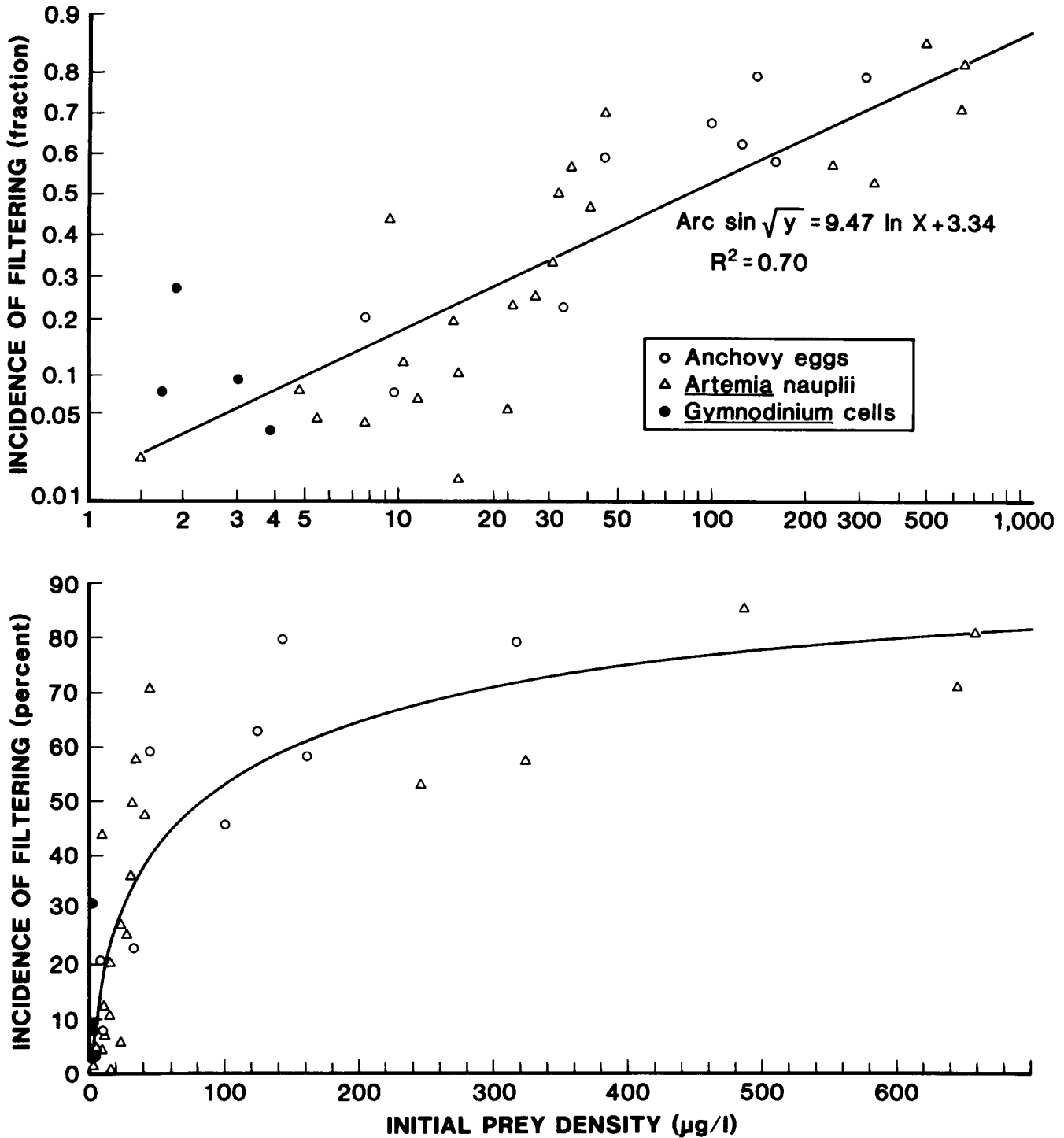


Figure 2. Mean incidence of filter feeding in northern anchovy schools during initial 9 min of feeding as a function of initial prey density in dry weight per liter. Data in Figure 1 have been converted from numbers per liter to dry weight per liter using the conversions, anchovy egg = 30.1 µg; *Artemia nauplius* = 1.70 µg; and *Gymnodinium cell* = 0.0117 µg. Upper panel, incidence of filter feeding plotted on arcsine transformed scale ($\text{arcsin } \sqrt{y}$) and dry weight per liter on \log_e scale; lower panel, both parameters plotted on arithmetic scales, line from equation in upper panel.

version to dry weight brought together the behavior observations made on the three foods even though they were taken at widely different particle densities (Figure 2, upper panel). Because many of the percentages

of fish filtering were near the extremes (<30 percent or >70 percent), we used the arcsine transformation of the fraction of fish filtering (Sokal and Rohlf 1969) and regressed the transformed fractions on the \log_e dry

weight of prey per liter. The form of the relation between incidence of filtering and dry weight of food per liter (Figure 2, lower panel), resembles the type II predator response of Holling (1965), i.e., a negatively accelerated rise to a plateau. Because of variability in our data, we cannot distinguish statistically between a type II and a type I predator response, which is characterized by a linear rise to a plateau.

The intensity of filtering in anchovy schools may be a function of the density of filterable biomass. Figure 2 indicates that similar responses to different foods occurred at the same density of biomass but not at the same particle density. Because we used only three foods, the results could also be attributed to specific food preferences, the prey weight proportionality being chance. On the other hand, *Artemia* might be expected to be the preferred prey because *Artemia* adults were a routine part of the laboratory diet, but the school responded much more strongly to eggs than to *Artemia* at low prey densities. We conclude that the density of biomass, regardless of prey type, is probably an important factor regulating the intensity of filter feeding in anchovy schools.

In contrast, the lowest concentrations of prey that stimulated filter feeding were inversely related to particle size or mass. A higher concentration of biomass per liter was required to elicit filtering of anchovy eggs than of *Artemia* nauplii, and a higher concentration of biomass was required to stimulate filtering of *Artemia* nauplii than was required for the much smaller particle *Gymnodinium* (Table 2). Threshold prey concentrations for initiating filter feeding are also inversely related to particle size in menhaden (Durbin and Durbin 1975). Thus the intensity of filtering by anchovy schools was proportional to the density of biomass in the water, whereas the threshold concentrations required to initiate filtering were inversely related to biomass. These findings may be explained in the following way. A higher concentration of biomass may be required for initiation of egg filtration than for filtration of *Gymnodinium* cells because at lower egg concentrations it is probably more efficient to bite rather than to filter eggs, whereas it is never efficient

to bite an individual *Gymnodinium* cell. In other words, the threshold density for initiation of filtering a particular prey may be a function of the cost of filtering relative to biting the prey, as well as of its mass; this would elevate the filtration threshold for larger filterable prey such as anchovy eggs, which may be profitably eaten either way.

In five preliminary experiments anchovy schools were given a high initial density of *Artemia* nauplii (29-322 nauplii/l), and the school was permitted to graze the food to low levels over an extended period. The incidence of filtering and the density of *Artemia* nauplii were recorded at intervals over the feeding period. In these experiments filtering activity remained at a high level even when the density in the tank was reduced below that required for the initiation of feeding. The average incidence of filtering at the end of the feeding period was 32 percent, by which time the density of *Artemia* had dropped to an average of 2 nauplii/l (Table 3). In contrast, the incidence of filtering was close to zero when nauplii at densities of 2-4/l were initially offered (see Figure 1, right panel). We observed the same behavior in anchovy that were fed eggs. The tendency for high levels of filtering to persist after nearly all food has been removed seems to be a common characteristic in filter-feeding clupeoids, for similar behavior has been observed in Atlantic menhaden (Durbin and Durbin 1975). Thus, anchovy schools that encounter a dense patch of prey may reduce the density below the threshold for initiation of feeding and consequently have a greater impact on the prey than indicated by filter-feeding thresholds.

DISCUSSION

A strong filtering response to eggs occurred at densities above five eggs/l, and the threshold for the onset of filtering (based on a detectable change in egg density) was between 1 and 2 eggs/l. The density of anchovy eggs in the sea, estimated from horizontal

TABLE 2
 Density Threshold Range for the Onset of Filter Feeding
 in Northern Anchovy

Food type	Particle size		Threshold for onset filter feeding	
	Dimensions μm	Dry weight μg	No/l	Dry wt (μg)/l
Anchovy eggs	1340 x 660	30.1	1-2	30-60
<i>Artemia</i> nauplii	433 x 236	1.7	5-18	8.5-31
<i>Gymnodinium</i>	40 x 40	.0117	151-328	1.8-3.8

TABLE 3
 Persistence of High Levels of Filtering of Northern Anchovy
 Schools Fed on Initially High Food Density

Initial density <i>Artemia</i> nauplii (n/l)	Initial incidence of filtering ¹ (percent)	Duration of feeding (min)	Final density <i>Artemia</i> nauplii (n/l)	Final incidence of filtering ² (percent)	School size (numbers of fish)
322	89	29	3.1	33	488
58	31	27	1.3	42	424
53	57	29	1.4	30	418
39	35	30	3.8	29	486
29	30	28	0.6	27	498
Mean 100	48	29	2.0	32	463

¹Measured over initial 9 min of feeding.

²Measured over last 2 min of experiment.

plankton tows, is typically two or more orders of magnitude below this filtering threshold. On the other hand, very high egg densities are occasionally recorded. The highest density of anchovy eggs taken in a neuston net was 31/l, corresponding to a density of 46,000 eggs/10 m² of sea surface, which compares with the upper 5 percent of all anchovy egg samples (ranked by density) taken in oblique tows (nylon nets) by the California Cooperative Oceanic Fisheries Investigations ichthyoplankton surveys (unpublished data Southwest Fisheries Center, La Jolla, California).

The integrating characteristic of plankton tows doubtless underestimates to some extent the peak densities of anchovy eggs actually encountered by an anchovy school. Further, the threshold based on density changes in our tank probably underestimates possible effects, because behavior observations indicated that at least some of the fish are stimulated to filter eggs at densities as low as 0.26 eggs/l. Finally, that as many as 730 eggs have been taken from a single anchovy stomach indicates that at times eggs are highly concentrated in the sea (Hunter and Kimbrell 1980). All of these factors point to the conclusion that at least occasionally anchovy egg densities are sufficiently high in the sea to stimulate filter feeding directly, but that eggs are probably also taken when fish are stimulated to filter by concentrations of other prey. It will require more accurate measurements of egg density in the sea to determine the extent of selective feeding on eggs.

Measurement of the size structure of zooplankton assemblages in front of and behind northern anchovy schools indicates that anchovy feed selectively by consuming relatively more of the larger prey and less of the smaller ones in an assemblage (Koslow 1981). The size of zooplankters selected by anchovy in Koslow's study were frequently less than 1 mm. Adult northern anchovy filter eggs (ca. 1.3 mm x 0.6 mm) and smaller particles, whereas they bite anchovy larvae in the yolk-sac stage (ca. 2.8-4.0 mm) and *Artemia* adults (5-10 mm); (Leong and O'Connell 1969). Since the transition from filtering to biting probably occurs at a prey size between 1 and 3 mm, Koslow's data indicate that selectivity results from filter feeding as well as biting.

At least three mechanisms could cause selectivity in filter feeding: selective ingestion, selective gaping, and selective orientation. Selective ingestion, retention on the gill rakers, and ingestion of a preferred prey might occur, but no evidence exists. On the other hand, the fineness and structure of the gill rakers establishes the minimum size of filterable prey; in a limited sense this could be considered selectivity.

Selective gaping was documented in this paper. Our

experiments indicated that the frequency or duration of filtering acts increased with the density of biomass (our behavioral observation methods do not distinguish between increases in frequency or duration of filtering acts, but they appear to covary). Thus, preferred prey can be selected by varying the intensity of filtration, and preferences appear to exist for large filterable prey or for smaller ones at an equivalent density of biomass. In addition, filtering persisted long after the density of prey was reduced to sub-threshold levels. This factor amplifies the effect of selective gaping.

Selective orientation of a school to patches of prey can also cause selectivity in filter feeding. When food (*Artemia* nauplii or anchovy eggs) was added to a small area in our test tank the anchovy would interrupt their circuit of the tank when they encountered the patch; at first the school would be disorganized, with individuals independently swimming rapidly in small elliptical orbits while filtering intensively in the area of the food patch. Soon this behavior would become synchronized, with the entire school swimming in a larger elliptical orbit through the food patch while continually filtering. Chemical stimuli alone are sufficient to elicit the first stages of this behavior (change in school direction with individuals swimming independently in small elliptical orbits), but filtering and formation of a well-organized school in the patch require the presence of food (C. Barnett, pers. comm.). Thus, food preferences based on chemical stimuli may cause changes in the direction of school movement that could lead to selective filter feeding.

In conclusion, northern anchovy schools may regulate filtering intensity in accordance with the concentration of filterable biomass in the water, and this probably results in selection of the larger prey in an assemblage. Selectivity also may be accomplished by the school's orientation to chemicals produced by a patch of prey. Since anchovy eggs are large relative to many planktonic foods and occur in dense patches, selective gaping and orientation probably occur. It would be of interest, in this regard, to determine if the intensity of filtering depends upon the largest and most abundant component in an assemblage or on the combined total of all filterable organisms.

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