

VISUAL THRESHOLD FOR SCHOOLING IN NORTHERN ANCHOVY *ENGRAULIS MORDAX*

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ABSTRACT

The visual threshold for schooling was determined for two groups of 50 adult northern anchovy in the laboratory. The index of dispersion and the mean distance to the nearest neighbor were used to measure changes in schooling as a function of light intensity. The threshold light intensity for schooling, 6×10^{-11} W cm⁻² (2.6×10^{-4} mc), was estimated to occur at a depth of 30 m on a starlit night and at 38 m during a full moon, when the chlorophyll concentration is 0.2 mg Chl a m⁻³. At 2.0 mg Chl a m⁻³ the threshold occurs at a depth of 8 m on a starlit night and at 20 m under full moon light. Sufficient light appears to exist at night within the upper 10 m for schooling to occur in most of the habitat of the anchovy. The vertical distribution of newly spawned anchovy eggs indicated that the maximum depth of spawning may be similar to the maximum depth of schooling and that the visual threshold for schooling could be used to forecast maximum spawning depth in the sea.

Vision plays a primary role in the maintenance of most fish schools in the sea. Other sense organs, particularly the lateral line, are important in coordinating movements and spacing of fish within the school (Pitcher et al. 1976), but it is unlikely that lateral line sense alone is sufficient for maintaining the integrity of schools at night in the sea. In fact, a large number of laboratory studies indicate that if light is sufficiently reduced, fish no longer maintain schools (Whitney 1969; Blaxter 1970). Thus the visual threshold for schooling and the depth of penetration of light probably determine the maximum depth at which pelagic fishes are able to school at night in the sea.

Our objective was to determine the visual threshold for schooling in adult northern anchovy, *Engraulis mordax*, and to use this information to forecast the maximum schooling depth for anchovy at night in the sea. This calculation is of ecological interest because the maximum depth for schooling is probably also the maximum depth for spawning and for nocturnal feeding. Anchovy spawn only at night and visual recognition of other fish is probably as essential for spawning as it is for schooling. During what we believe was spawning behavior, several males rapidly pursued a female over an irregular path, a tactic probably not possible using senses other than vision. This is a casual laboratory observation and requires further documentation, however.

Northern anchovy feed at night as well as in the day (Loukashkin 1970; Hunter and Kimbrell 1980). Light may not be necessary for filter feeding, but it is essential for particulate feeding, although somewhat higher light levels may be required for feeding than for schooling (Hunter 1968). Anchovy migrate toward the surface at sunset (Mais 1974), and schools are less frequently detected at night using sonar and not detected with echo sounders (Smith 1970). Nevertheless, no doubt exists that schooling continues at night because the anchovy fishery is typically a night fishery and because profiles of schools are detectable at night owing to the bioluminescent disturbances their movements produce (Squire 1978).

METHODS

Apparatus and Laboratory Procedures

Two groups of 50 northern anchovy (group 1, mean length = 10.5 cm SL; group 2, = 9.8 cm SL) were maintained in a 4.6 m diameter tank supplied with running seawater (group 1, mean temperature = 16.9°C; group 2, 21.0°C). To simplify photographic analysis the school of 50 fish was constrained to a somewhat two dimensional form by maintaining them in water 45 cm deep. The fish were fed adult *Artemia* at the daily time of 1000, and the tank was cleaned 1 h after feeding.

The tank, which was constructed of blue vinyl, was located in a light tight rectangular enclosure in which the walls and ceiling were covered with white vinyl

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to diffuse the light. Four light sources were equally spaced around the periphery of the tank; the top of each being just below the tank rim. Each source consisted of a 30 W tungsten microscope lamp with reflector enclosed in a tube. On top of the tube were two color filters; a green acrylic plastic filter (#2414, Rohm and Haas), and a sealed petri dish containing a 5% CuSO₄ solution (by weight). To diffuse the light a translucent white acrylic filter (#W-2447, Rohm and Haas) was placed on top of the color filters and light transmitted by the white filter entered a white opal glass globe (13 cm diameter) that formed the top of the source. The lamps were operated for 5 h (10% of lamp life) before they were used to produce test levels of irradiance. These sources were used to produce four test levels of irradiance during a 12-h night. Additionally, four tungsten 100 W household lamps (unfiltered) with reflectors were used for the daytime level of irradiance. These lamps were placed at regular intervals around the perimeter of the tank near the ceiling. Light from these lamps reflected off the ceiling providing a uniformly diffuse illumination. The spectrum produced by the four sources (Table 1) resembles the greenish spectrum typical of anchovy habitat, but the spectrum used in the day was not different from a standard curve for a tungsten lamp and consequently contained an unnaturally high proportion of longer wavelength energy. Our term for the condition when all lamps were off was darkness; under these conditions light was not detectable by a dark adapted human observer and the irradiance was below the sensitivity of a 931A photomultiplier which can detect about 5×10^{-6} mc (meter candle).

To record the effect of light on the schools the fish were photographed from above the tank using a 35

mm automatic camera and flash attachment. The camera was controlled by a timer, and photographs were taken at 30-min intervals for 5 h during the 12-h day, at night in darkness, and at night at the test levels produced by the four sources. Night photographs were taken during a 5-h period commencing 2 h after the end of the 12-h day. Ten photographs were usually analyzed at each light level for each group, but in several tests, 1 or 2 photographs were not analyzed because not all 50 fish could be seen.

Two indices of schooling were calculated for each photograph: an index of dispersion (Pielou 1969), and the mean distance to the nearest neighbor (Hunter 1966). The dispersion index was calculated by superimposing a grid containing 326 quadrats over the projected image of the tank and counting the number of fish occurring in each quadrat. The variance mean ratio (s^2/\bar{x}) for the number of fish per quadrat was the index of dispersion. The index was calculated for each photograph, and an average index was computed for each light treatment ($n = 8-10$ photographs). A dispersion index of 1 indicates a random distribution, whereas higher values indicate aggregation (Pielou 1969) and imply the existence of schooling. Values < 1 imply a uniform distribution over the grid. The mean distance to the nearest neighbor was computed for a random subsample of 10 fish in a photograph. All 50 fish in a photograph were numbered and the subsample of 10 was selected by drawing the fish numbers from a table of random numbers. For each of the 10 fish in the subsample the distance in centimeters to its nearest neighbor was measured (distance between heads), a mean distance calculated for each photograph, and means

TABLE 1.—Spectral functions used to estimate the depth of occurrence of the visual threshold for schooling under the various water types and incident irradiances including spectral irradiance in the laboratory apparatus, moonlight at 3 m below water surface, starlight at the earth's surface (Munz and McFarland 1977), and the relative sensitivity of the dark adapted anchovy eye (*Engraulis encrasicolus*, Protasov 1964).

Wavelengths (nm)		Energy per 25 nm interval (W cm ⁻²)			Relative sensitivity anchovy eye
Mean	Interval luminaires	Laboratory luminaires	Moonlight at 3 m depth	Starlight at surface	
400	400-412	3.411×10^{-12}			
425	413-437	1.346×10^{-11}	6.109×10^{-10}	1.978×10^{-11}	0.16
450	438-462	3.402×10^{-11}	6.689×10^{-10}	2.418×10^{-11}	0.53
475	463-487	6.822×10^{-11}	6.820×10^{-10}	2.291×10^{-11}	0.85
500	488-512	9.631×10^{-11}	7.072×10^{-10}	2.374×10^{-11}	1.00
525	513-537	1.069×10^{-10}	7.067×10^{-10}	2.449×10^{-11}	0.75
550	538-562	9.618×10^{-11}	7.283×10^{-10}	5.125×10^{-11}	0.42
575	563-587	5.297×10^{-11}	6.881×10^{-10}	2.838×10^{-11}	0.22
600	588-612	9.494×10^{-12}	5.481×10^{-10}	3.874×10^{-11}	0.08

¹Wavelength interval = 588-600 nm.

for each light treatment. These measurements are indices of only one characteristic of a fish school, the tendency of individuals to maintain contact with each other and thereby remain in a social group. The polarization of individuals in a school is frequently included in definitions of schooling as the cohesive movements of a school require that fish maintain relatively constant headings and individual distances which gives the polarized appearance of moving schools. This characteristic of fish schools was not measured in our study, thus the visual threshold we estimated was one for the maintenance of schooling in the broadest sense, that is the existence of a group maintained by visual attraction.

Radiometric Procedures, Calibrations, and Computations

Radiometric equipment used in this study consisted of an Optronics spectroradiometer (model 714-V) (calibrated against a radiometric standard) and a photometer (Gamma Model 700). The spectroradiometer was used to measure the spectral irradiance produced by the sources at full lamp output but the treatment levels of irradiance were below the sensitivity of the spectroradiometer. Absolute measurements of light intensity were made 25 cm above the water surface (the difference between this position and within the water would be < 10%). The light treatments were varied by placing neutral density filters in each of the light sources; the neutral density filters were calibrated on an optical bench. Test levels we used were computed from the filter factors for the neutral density filters. The photometer was used to check irradiance levels prior to a test, but we believe the computed values to be more accurate. Irradiance distribution in the tank was mapped using the photometer and the treatment values weighted by tank area so that they represented the average irradiance 25 cm above water surface.

Our laboratory estimates of the visual threshold for schooling were used to calculate the maximum possible depth of schooling in the sea for various levels of incident irradiation and water types. Threshold values in $W\text{ cm}^{-2}$ were converted to anchovy effective units ($W\text{ cm}^{-2}_{\text{anch. eff.}}$) by weighting the spectrum in the apparatus by the relative sensitivity of the scotopic curve of the anchovy *Engraulis encrasicolus* from an electroretinogram by Protasov (1964) (Table 1). Two levels of night illumination were used, full moon at 3 m depth ($2.78 \times 10^{-9} W\text{ cm}^{-2}$), and starlight at the earth's surface ($1.08 \times 10^{-10} W\text{ cm}^{-2}$) (both measurements from Munz and

McFarland 1977). The depth (meters) in the sea (Z) at which a given threshold (E_z) value occurred was calculated using the equation of Baker and Smith (1982):

$$Z = \frac{\ln \left(\frac{E_z}{E_0} \right)}{-K_t}$$

where E_0 is the incident radiation (full moon or starlight) in anchovy effective units. K_t is the wave length specific attenuation coefficient and is the sum of coefficients for pure water (K_w), dissolved organic matter (K_d), and chlorophyll a (K_c). Tables of coefficients, and equations for calculating these attenuation coefficients, are given by Baker and Smith (1982). In our calculations we assumed that the dissolved organic matter was constant at 0.7 mg l^{-1} which is typical of the anchovy habitat. We calculated K_c for a range of chlorophyll (Chl) a concentrations ranging from 0.1 to 10 mg Chl a m^{-3} and at 25 nm intervals from 425 to 600 nm for each Chl a concentration. Each K_t value for 25 nm increments was weighted by the appropriate anchovy scotopic sensitivity, and the average anchovy weighted $K_{t, \text{anch. eff.}}$ was used in the final calculation of Z .

Many uncertainties and possible biases exist in such an extrapolation from laboratory to sea conditions: Cloud cover was not considered nor were possible effects of bioluminescence; spectral irradiance values for full moon and starlight of Munz and McFarland (1977) may not be representative of conditions in the anchovy habitat although they are relatively close to those given in photometric units by Brown (1952); variation in dissolved organic matter is not considered; the radiance distribution over 360° in the tank probably does not resemble that in the sea (only downwelling irradiance was considered here); use of the action spectrum based on an electroretinogram of a dark adapted *E. encrasicolus* eye instead of one for schooling of *E. mordax*; and of course, the usual statistical uncertainties. Despite these uncertainties and biases we believe our estimates of schooling depth are the most accurate to date thanks to the models developed by Baker and Smith (1982).

RESULTS AND DISCUSSION

The schooling threshold based on the index of dispersion was between 4.8×10^{-12} and $7.8 \times 10^{-10} W\text{ cm}^{-2}$ (Fig. 1; Table 2). At the lower value and in darkness the index of dispersion (s^2/\bar{x} fish per

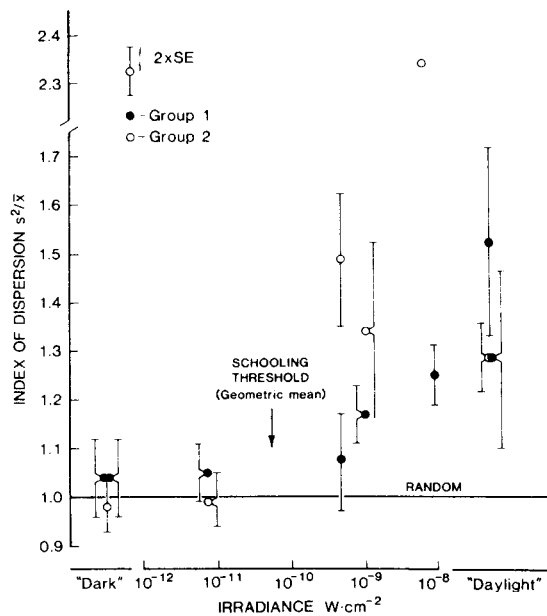


FIGURE 1.—Visual threshold for schooling in northern anchovy. Schooling is indicated by the index of dispersion (s^2/\bar{x}). A ratio of 1 implies no schooling as it indicates a random distribution. Each point is a mean calculated from 8-10 photographs and bars are $\pm 2 \times$ standard error of the mean. No error bars are given for one value (2.34 ± 0.47) because it falls far beyond the rest of the values. Mean dispersion is shown for four test levels of downwelling irradiance (log scale), "dark" (below the sensitivity of a 931A photomultiplier), and "daylight" ($1.496 \times 10^{-5} \text{ W cm}^{-2}$) which was the normal daytime level of irradiance in the apparatus.

quadrat) did not differ from unity indicating that the fish were randomly distributed. Hence no schooling existed at the lower irradiance value and in darkness, whereas at the higher value the fish were clearly aggregated. These values delimit a region of about 2 log units of irradiance where one cannot be certain if schooling occurs or not. The actual threshold for schooling must fall somewhere in that region, and we have arbitrarily considered the threshold value to be the geometric mean irradiance of the above two irradiances ($6 \times 10^{-11} \text{ W cm}^{-2}$) thereby reducing the uncertainty in the threshold value to about 1 log unit. In subsequent tables and figures we give the upper and lower bounds of the region as well as the threshold value, however.

The variance of the dispersion index, a measure of the variation in school dispersion among photographs, increased sharply at irradiances above the threshold indicating a wide variation in the dispersion of fish among photographs. This can be expected because schooling fish react to fright stimuli, feeding, and many other conditions by altering interfish distances, thereby changing the cohesion or degree of dispersion of the school (Blaxter and Hunter 1982). At light levels below the visual threshold, fish are unable to respond socially to such stimuli, hence the variation among photographs is low.

Mean distance to the nearest neighbor followed the same pattern as we have described for the index of dispersion. Values in darkness and at the lower

TABLE 2.—Mean and standard deviation of the index of dispersion and mean distance to the nearest neighbor for various irradiance levels.

Irradiance (W cm^{-2})	Group	Schooling indices				Number of photographs
		Dispersion index (s^2/\bar{x})		Mean distance to nearest neighbor (cm)		
		\bar{x}	s	\bar{x}	s	
1.496×10^{-5} ("daylight")	1	1.28	0.29	17.50	3.71	10
	1	1.52	0.30	12.15	4.10	10
	2	1.28	0.11	24.61	4.94	10
8.92×10^{-9}	1	1.25	0.10	12.19	2.52	10
	2	2.34	0.74	19.49	5.50	10
1.079×10^{-9}	1	1.17	0.09	16.65	3.86	10
	2	1.34	0.27	21.72	7.14	10
4.777×10^{-10}	1	1.07	0.15	18.48	3.86	9
	2	1.49	0.21	18.05	6.62	10
7.785×10^{-12}	1	1.05	0.09	21.87	5.39	8
	2	0.99	0.07	30.40	5.14	10
Dark ³	1	1.04	0.12	21.20	4.16	9
	1	1.04	0.12	19.61	4.83	9
	2	0.98	0.07	34.12	6.36	10

¹Unfiltered tungsten lamp.

²Filtered lamp - spectrum given in Table 1.

³Below sensitivity of 931A photomultiplier.

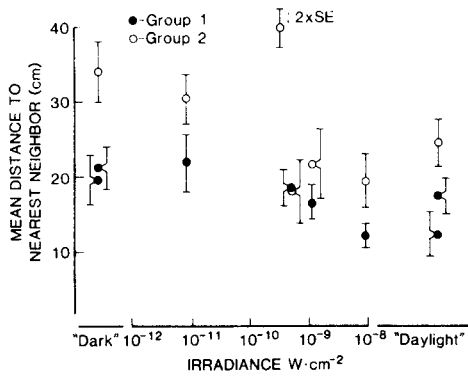


FIGURE 2. - Visual threshold for schooling in northern anchovy is indicated by changes in the mean distance to nearest neighbor. Each point is a mean calculated from 8-10 photographs and bars are $\pm 2 \times$ standard error of the mean. Mean distance to the nearest neighbor is shown for four test levels of irradiance (log scale), "dark" (below the sensitivity of a 931A photomultiplier), and "daylight" ($1.5 \times 10^{-5} \text{ W cm}^{-2}$) which was the normal daytime level of irradiance in the apparatus.

irradiance values were not statistically different. Above the threshold the mean distance to nearest neighbor was lower than that in darkness indicating closer spacing among pairs, but no trend with light intensity seemed to exist above the threshold range (Fig. 2). For the purpose of estimating a threshold, however, we believe the index of dispersion is preferable because the criterion for randomness is well defined and the dispersion index takes into account all 50 fish, whereas we used only 10 random pairs per photograph for the nearest neighbor measurements which reduced its precision.

Our calculations indicate that in water of low chlorophyll concentration ($0.2 \text{ mg Chl a m}^{-3}$) the threshold irradiance for schooling occurs at a depth of 38 m during a full moon and at a depth of 30 m on a starlit night (Fig. 3). The method of calculation is described in the Methods section on radiometric procedures. Light attenuates rapidly as Chl a concentration increases up to about 2 mg m^{-3} total chlorophyll; at $2.0 \text{ mg Chl a m}^{-3}$ the schooling threshold occurs at a depth of only 8 m on a starlit night and at 20 m under full moonlight. Above $2 \text{ mg Chl a m}^{-3}$ light attenuates more slowly with increasing Chl a concentration with the threshold at $10 \text{ mg Chl a m}^{-3}$ falling at 5 m in starlight and at 12 m in full moonlight. These calculations indicate that sufficient light exists at night for northern anchovy to school within the upper 10 m of nearly all habitats under clear skies, but the maximum possible depth of the schooling would be expected to vary greatly with water

type and incident light intensity. An order of magnitude decline in incident irradiation can be expected under the darkest storm clouds (Brown 1952); under these conditions schooling may not be possible at the highest chlorophyll concentrations.

It seems appropriate to use these visual thresholds as estimates of the maximum depth of spawning because spawning probably also depends upon the ability of anchovy to see one another. We calculated the vertical distribution of newly spawned anchovy eggs (0-4 h old, type "S") using data from the unpublished vertical distribution study of Pommeranz and Moser (1983). We selected sets of vertical samples at two stations for which surface Chl a concentrations had been measured and then calculated a mean Chl a concentration for an inshore and offshore series of net hauls. We then estimated the maximum depth for schooling assuming that the surface Chl a was equivalent to an integrated value for the water column as required by the Baker and Smith 1982 model. Spawning occurred closer to the surface at the inshore station which had a high Chl a concentra-

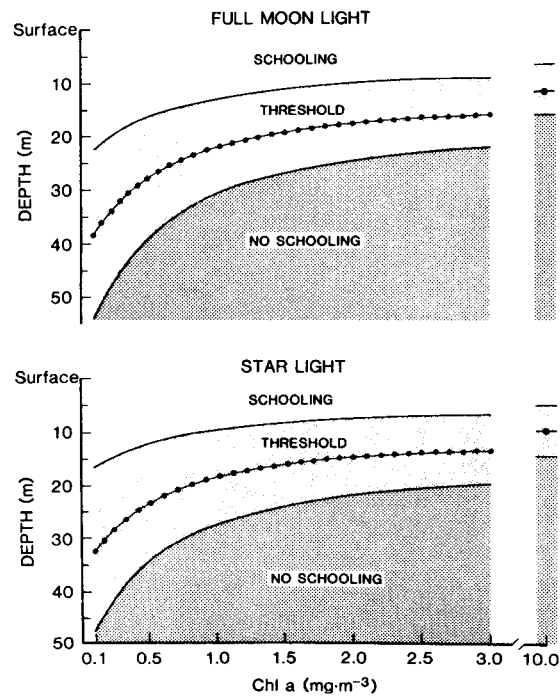


FIGURE 3. - Maximum depth of schooling of northern anchovy in waters of various chlorophyll concentrations (Chl a) under starlight and full moon. Coefficients used in calculations are in Table 1 and in Methods section. Darkly shaded area indicates proportion of water column where no schooling is expected, lightly shaded area indicates depth range of schooling threshold. Central dotted line is the geometric mean.

tion (1.5 mg m^{-3}) than at the offshore station which had a lower concentration ($0.24 \text{ mg Chl a m}^{-3}$). At the onshore station only 4% of the eggs occurred below 20 m, whereas at the offshore station 31% were below 20 m. This difference is particularly striking because the inshore samples were taken under a full moon, whereas the moon was in the first quarter when the offshore station was occupied. At both stations the predicted maximum depth for schooling was close to the observed maximum depth for newly spawned eggs (Fig. 4). We may have underestimated the depth of schooling for the offshore (low Chl a) station as we used a starlight value of Munz and McFarland (1977) because no data existed for 1/4 moon. Spawning occurred prior to moonset since spawning occurs between the time of 1800 and 2400 and moonset varied from about the time of 2130 to 0200 (19-25 March 1980). In addition, the offshore station had a deeper mixed layer (about 35 m) than the inshore station (about 10 m) and vertical distribution of anchovy eggs and larvae also may be affected by the depth of the mixed layer (Ahlstrom 1959). Regardless of these uncertainties, these data indicate that underwater visibility may set the maximum depth for spawning of anchovy,

although other factors, such as low temperature, might constitute an additional barrier to spawning schools. Thus fish visual thresholds may be a convenient way to establish a general function for estimating the maximum depth of spawning for anchovy and perhaps other pelagic spawning clupeoids in all habitats. Such a general function, that could account for much of the variation in the maximum depth of eggs, could be quite useful in three dimensional models of larval transport or predation. A spawning-depth, water-type function based on visual thresholds seems particularly attractive owing to the considerable cost of accurately measuring the vertical distribution of eggs and larvae even in a single habitat let alone the cost for estimating it for all possible spawning habitats of the population.

To compare the northern anchovy schooling threshold to literature values we converted our radiometric measurements to lux or meter candles (mc), by weighting the spectral irradiance in the apparatus by the human photopic curve, as the literature values are largely in photometric units (see reviews by Whitney 1969 and Blaxter 1970). The visual threshold for anchovy schooling ($2.6 \times 10^{-4} \text{ mc}$, Table 3) is about an order of magnitude higher

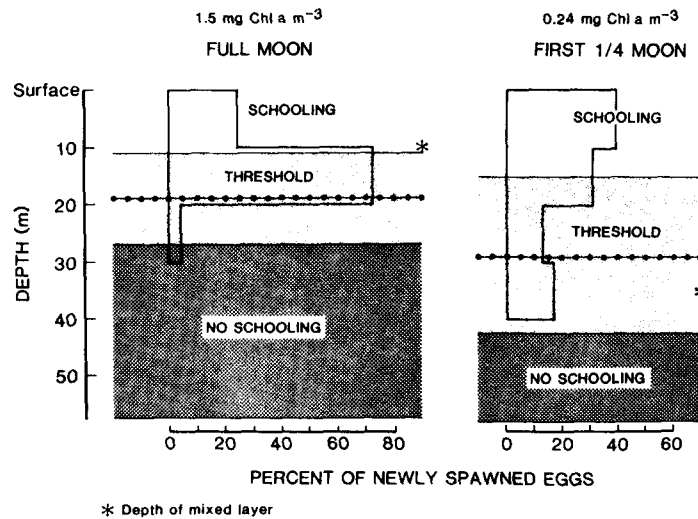


FIGURE 4.—Comparisons of the estimated depths of schooling of northern anchovy and the observed depths of spawning. Estimated depth of schooling calculated from visual threshold estimates ($W \text{ cm}^{-2} \text{ anch. eff.}$), an assumed dissolved organic matter of 0.7 mg l^{-1} , and the average Chl a concentration and moon phase at the station (1/4 moon phase assumed to be equivalent to starlight) using the model of Baker and Smith (1982). Observed spawning depths at the two stations are indicated by a frequency histogram for newly spawned anchovy eggs where the y axis indicates the depth stratum of the plankton tow and the x axis indicates the percentage of newly spawned eggs taken at each of the 10 m vertically stratified tows. Data are from Pommeranz and Moser (1980) and are for the total number of newly spawned eggs taken over a 4-8 d interval.

TABLE 3.—Upper and lower bound and geometric mean for the visual threshold for schooling of adult northern anchovy, *Engraulis mordax*, in the various energy units.

Energy units	Schooling ¹	No schooling ²	Geometric mean ³
Radiometric (W cm ⁻²)	4.777 × 10 ⁻¹⁰	7.785 × 10 ⁻¹²	6.051 × 10 ⁻¹¹
Anchovy effective* (W cm ⁻² _{anch. eff.})	3.079 × 10 ⁻¹⁰	5.018 × 10 ⁻¹²	3.900 × 10 ⁻¹¹
Photometric ⁵ (mc)	2.048 × 10 ⁻³	3.337 × 10 ⁻⁵	2.594 × 10 ⁻⁴

¹Lowest irradiance level at which schooling occurred.

²Highest irradiance level at which anchovy failed to school.

³Geometric mean of the irradiance at the upper and lower bounds of the threshold.

⁴Weighted by ERG action spectra for *Engraulis encrasicolus* dark adapted retina (413-612 nm) (Protasov 1964).

⁵Weighted by the 1964 human photopic response (413-600 nm).

than that for jack mackerel (3.5×10^{-5} mc, Hunter 1968), a species associated with anchovy in the California Current. Visual thresholds for schooling in fishes range from about 1×10^{-5} to 1×10^{-1} mc with about 90% (14/16) of the literature values being higher than anchovy (Blaxter 1970). We do not attach much importance to such specific differences because criteria for schooling differ widely and radiometric procedures in the older studies were primitive by today's standard. We suspect the threshold for jack mackerel may have been lower than the northern anchovy because of use of a uniform and highly reflective background in the apparatus and the use of photometric brightness as a unit of measurement. In our work the brightness to the sides and below was much lower than the downwelling irradiation whereas this was not the case in the jack mackerel experiment.

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