

## THE ONSET OF SCHOOLING IN NORTHERN ANCHOVY LARVAE, *ENGRAULIS MORDAX*

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### ABSTRACT

Laboratory measurements indicate that schooling begins in larval northern anchovy when they are between 11 and 12 mm standard length and is well established when they reach 13-15 mm. The onset of schooling closely parallels an increase in patchiness of larvae in the sea, and it begins during the period that larvae form a duplex retina and undergo major changes in their respiratory and locomotor systems.

### RESUMEN

Observaciones sobre larvas de *Engraulis mordax* en el laboratorio indican que la formación de cardúmenes se inicia cuando las larvas alcanzan de 11 a 12 mm de longitud normalizada, y el cardumen ya está bien definido en larvas de 13 a 15 mm de longitud. La formación del cardumen se produce coincidiendo bastante con el período en que la distribución de las larvas en el mar muestra un incremento en la formación de agrupaciones, y además se inicia cuando la larva adquiere una doble retina y experimenta cambios notables en sus sistemas respiratorio y natatorio.

### INTRODUCTION

Except for a portion of the larval stage, all life activities of northern anchovy—feeding, avoiding predators, migrating, and reproducing—are conducted within schools. Thus the time at which schooling begins is an important event in the life history of anchovy, for it identifies the first time that they may be able to profit from schooling. In the larval stage the most important benefit of schooling may be a reduction in predation and cannibalism, although facilitation of the search for food and timing of vertical migration might be additional benefits. For example, fry of the freshwater fish *Gobiomorus dormitor* have a 30 percent chance of being eaten when alone, whereas one individual in a school has a chance of less than 1.5 percent (McKaye et al. 1979). Thus, identifying the larval size at which schooling begins is necessary to properly understand the effects of predation, cannibalism, and food abundance on size-specific mortality rates.

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Our objective was to identify the period when schooling begins, by observing the behavior of northern anchovy larvae reared in the laboratory. The ontogeny of schooling behavior has been studied in detail in *Menidia menidia* by Shaw (1960 and 1961) and Williams and Shaw (1971), in *Atherina mochon* by Journé-Safriel and Shaw (1966) and Williams (1976), and in various cichlids by Dambach (1963). The focus of these past studies was on describing the development of this behavior, the effects of isolation, and the behavioral mechanisms underlying school development. Our focus was more limited, as we wished simply to determine the minimum larval size or age at which schooling might be expected to begin in the sea. Thus larvae were maintained in large communal rearing containers rather than in isolation, and behavioral measurements were designed to identify the onset of schooling but not to understand the underlying behavioral mechanisms.

### METHODS

#### Culture

Three groups of anchovy larvae were reared on a diet of *Gymnodinium splendens*, *Brachionus plicatilis*, and the harpacticoid copepod *Tigriopus californicus*, using methods outlined by Hunter (1976). Eggs were obtained from the induced spawning of fish maintained in the laboratory (Leong 1971). Three thousand eggs were stocked in each of three black fiberglass cylindrical tanks (122 cm diameter, 36 cm deep); the initial water depth was 18 cm (200 l) and increased from daily additions of seawater containing algae and food to about 400 l in about 20 days. Larval density in the three tanks during the time schooling occurred were 3.5 larvae/l (group 1), 1.7 larvae/l (group 2), and 4.3 larvae/l (group 3). In group 3 the water volume of the tank was reduced just before the behavior observations were begun, increasing the density from 2.1 to 4.3 larvae/l. Larvae were not transferred but were observed directly in the rearing tank. Each tank received about 2000 mc at the surface for 12 hours and dark for 12 hours; water temperature was maintained between 15.6 and 16.4°C. Ten or more larvae were sampled every other day to measure growth, and the daily change in schooling behavior was expressed as a function of mean larval length.

**Indices of Schooling Behavior**

In active fishes such as the northern anchovy, schooling produces cohesive groups in which the individuals maintain more or less parallel orientation. In some species of schooling fishes, parallel orientation may not be a good index of schooling, but in anchovy it is a natural consequence of their continuous movement and mutual attraction. Thus as schooling develops in larval anchovy, the social attraction among individuals will become stronger, groups or pairs will be more cohesive (remain together for longer periods), individuals will approach one another more often by parallel alignment, and parallel orientation will persist for longer periods. To measure the onset of schooling in larval anchovy we used three indices of these schooling characteristics: frequency of parallel orientation, the cohesion of pairs, and pair cohesion with parallel orientation.

Each morning seven individual larvae were observed for 5 minutes each; another seven were observed in the same manner for 5 minutes each afternoon. Observations were taken at least 2 hours after food was added to the tank. Daily observations began when larvae reached 10-13 mm and ended when the schools became highly reactive to the observer's presence. Interactions of the selected larva with other larvae in the rearing container were recorded with a keyboard and a multiple-pen event recorder. An interaction was defined as an encounter between a selected larva and another larva at a distance of 1 body length or less (a 1-cm grid etched on the bottom of the tank was used to judge distances). The duration of each interaction (seconds the pair remained at 1 body length) was recorded, as was the orientation of the interacting pair. Orientation was classified (Figure 1A) as (a) parallel (aligned side by side or head to tail); (b) head-to-head; and (c) perpendicular (aligned body to head). If the initial encounter were head-to-head or perpendicular, but subsequently one larva followed the other, resulting in parallel alignment, the event was classed as parallel orientation. The frequency of parallel orientation was estimated for each larva by calculating the percentage of all parallel interactions. The cohesion of pairs was estimated by calculating the total time the selected larva was within one body length of any other larva (regardless of orientation) and expressed as a percentage of the total observation time (5 minutes). Pair cohesion with parallel orientation was estimated by calculating the total time the selected larva was parallel to and swam within one body length of any other larva; this was expressed as a percentage of the total observation time. Means for each of these three indices were calculated for each daily set of 14 larval observations.

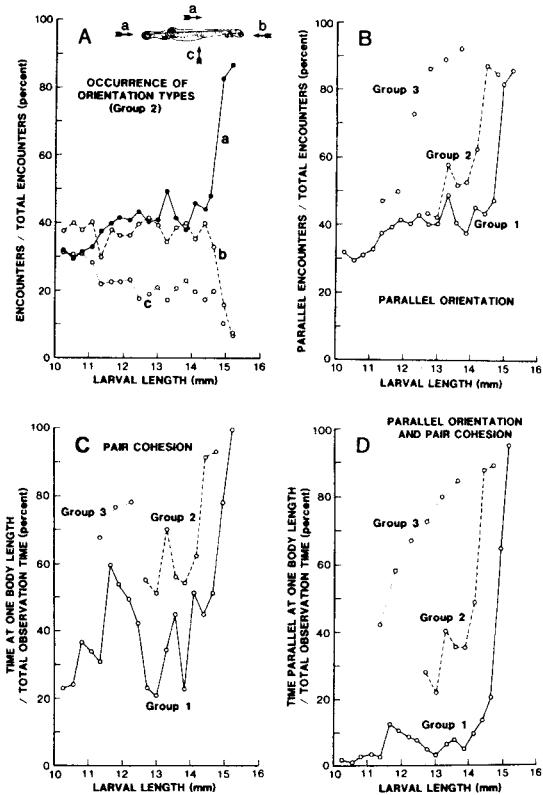


Figure 1. Indices of schooling as a function of the mean length of larval northern anchovy in three rearing containers (groups 1, 2, and 3). Each point is the mean of 14 five-minute behavior observations on different larvae.  
 A. Percentage occurrence of the three orientation classes during encounters between an observed larva and other larvae in group 2; orientation classes illustrated at top of panel: a, parallel; b, head to head; and c, perpendicular.  
 B. Percentage of encounters in which parallel orientation occurred in groups 1-3.  
 C. Percentage of the observation time a larva was within 1 body length of another larva (regardless of orientation).  
 D. Percentage of the observation time that a larva was aligned parallel to and swimming within one body length of another larva.

**RESULTS**

Larvae began showing signs of parallel orientation when they reached between 11 and 12 mm standard length. Before this time, when a larva approached another larva head on or perpendicular to the body, one of the pair would dart away in the opposite direction or occasionally would continue in a straight path showing no change in behavior. When larvae reached 11-12 mm a perpendicular approach often resulted in a turn by one of the larvae and a brief period of parallel swimming. Such events were scored as parallel encounters, although the initial approach was not parallel. The frequency of these encounters increased rapidly as the larvae grew (Figure 1 A, B). A sharp increase in the frequency of parallel encounters oc-

TABLE 1  
 Percentage of Observation Time Larval Northern Anchovy in Groups 1, 2, and 3<sup>1</sup> Were Schooling at Various Ages and Mean Lengths

Larval length <sup>3</sup> (mm)	Group 1			Group 2			Group 3		
	Larval age (days)	Schooling <sup>2</sup> (percent)		Larval age (days)	Schooling <sup>2</sup> (percent)		Larval age (days)	Schooling <sup>2</sup> (percent)	
		mean	2XSE <sup>4</sup>		mean	2XSE <sup>4</sup>		mean	2XSE <sup>4</sup>
10.3				16	2	1			
.4									
.5				17	1	1			
.6									
.7									
.8				18	3	1			
.9									
11.0									
.1				19	3	1			
.2									
.3							23	42	19
.4				20	3	1			
.5									
.6				21	13	4			
.7									
.8							24	58	29
.9				22	11	3			
12.0									
.1									
.2				23	9	4			
.3							25	67	28
.4									
.5				24	8	3			
.6									
.7	31	28	11	25	5	2	26	72	12
.8									
.9									
13.0									
.1	32	22	7	26	3	1			
.2							27	80	13
.3	33	40	11	27	7	2			
.4									
.5									
.6	34	35	15	28	8	3	28	85	14
.7									
.8				29	5	3			
.9	35	35	14						
14.0									
.1				30	10	2			
.2	36	48	14						
.3				31	14	6			
.4	37	88	14						
.5									
.6									
.7	38	88	15	32	20	7			
.8									
.9				33	65	13			
15.0									
.1									
.2				34	95	4			

<sup>1</sup>Larvae were first observed at age 31d (group 1), 16d (group 2), and 23d (group 3).

<sup>2</sup>Percentage of observation period pairs are at 1 body length and swimming parallel.

<sup>3</sup>From regression of larval standard length on age in each group rounded to the nearest 0.1 mm.

<sup>4</sup>2 X standard error of the mean where N = 14.

curred between 12 and 14 mm, depending on the laboratory group. By 15 mm all laboratory groups showed a strong schooling response. At this time they also became much more reactive to movements of the observer, although we moved as little as possible.

Within a particular group the three indices of schooling behavior (Figure 1 B, C, and D) showed the same trend with larval length ( $r^2$  values for comparisons between pairs of indices within each of the three experimental groups ranged from 0.72 to 0.99). Thus

to document the rest of this presentation we shall use only one index, the percentage of time spent swimming at one body length in parallel orientation (Figure 1 D). This index incorporates both the cohesive and the orientation properties of school structure. We also give the error terms for this index in Table 1, but for clarity they are deleted in Figure 1.

The timing of the onset of schooling varied among the three groups. It was the earliest in group 3 where the index for cohesion with parallel orientation attained values of 80-90 percent at 13.3 mm (age 27 days). Comparable values for group 1 occurred at 14.4 mm (age 37 days) and in group 2 at 15.2 mm (age 34 days).

Thus schooling had become clearly established in anchovy larvae by the time they attained a length of 13 to 15 mm. In other words, 13-15-mm larvae swam parallel to their neighbors at about a body length apart for 80-90 percent of the observation time. In group 3

the water in the tank was reduced by one-half when the larvae averaged 11.4 mm. After this disturbance the larvae immediately began to show signs of schooling, and they formed a relatively uniform school by 12.5 mm. It is not known if the increase in larval density (by a factor of 2) caused the early onset of schooling in group 3. The timing of the onset of schooling in the other two larval groups displayed a reverse pattern with larval density. We are more inclined to believe that the disturbance of changing the water and the resulting fright response induced an early onset of schooling. Examination of Figure 1 D or Table 1 indicates that the rate of change was more rapid in groups 1 and 2, where the onset of schooling began at somewhat longer length. This may indicate that the capability for schooling develops between 11 and 12 mm, but that external stimuli, perhaps a fright response, trigger the behavior. Schooling was not obvious in any group until 1 to 1½ hours after feeding, and if food

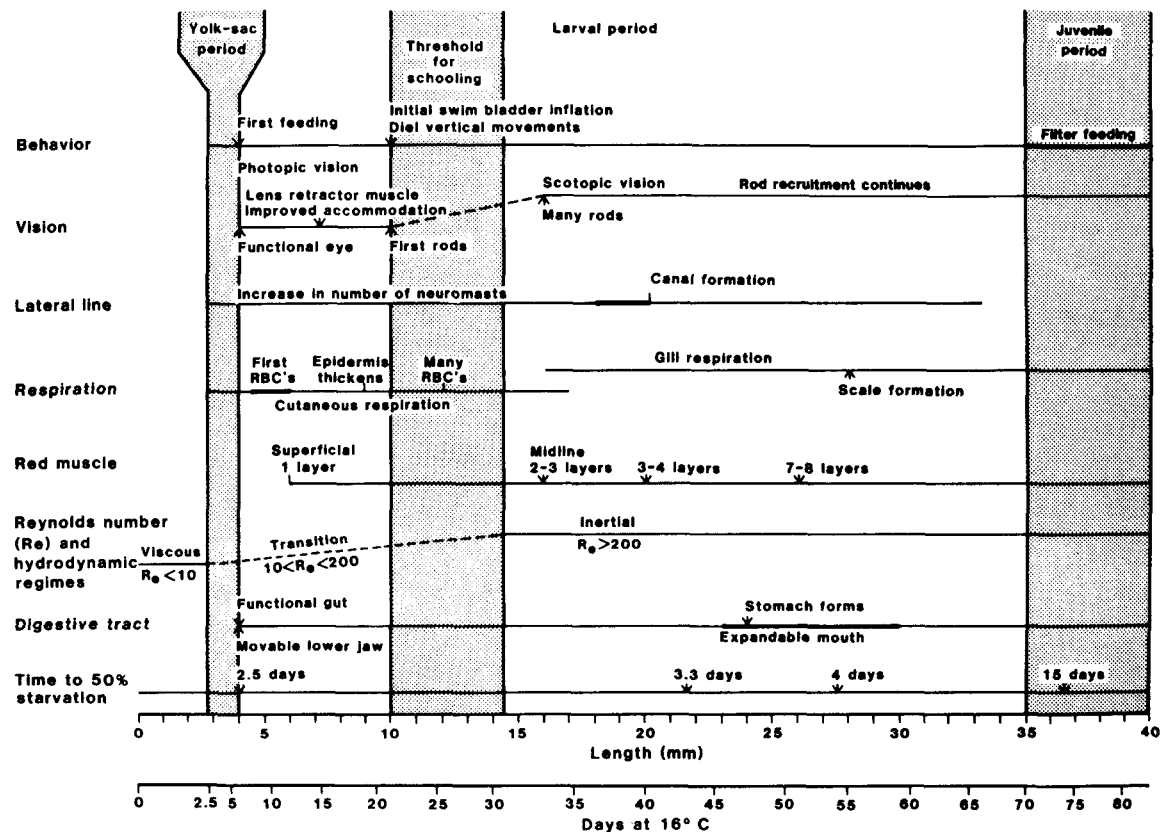


Figure 2. The timing of the onset of schooling in relation to events in the maturation of northern anchovy larvae. Structural events are from O'Connell (1981); hydrodynamic events from Weihs (1980); and all others from Hunter (1976), and Hunter unpublished data. RBC = red blood cells. Time to 50 percent starvation is number of days of starvation at which 50 percent of the fish died.

was insufficient the larvae appeared not to school. All data presented here were taken at least 2 hours after feeding on an abundant supply of food.

## DISCUSSION

The size of anchovy larvae at the onset of schooling is about the same as that determined for the marine silversides *Menidia*. Schooling (swimming continuously as a group) in *Menidia* is clearly established when they reach 10-12 mm (about 20 days old) (Shaw 1960; Williams and Shaw 1971). The period in larval development at which schooling begins is probably partially a function of the maturation rates of organ systems. Anchovy of this size (12-15 mm) are characterized by rapid structural and behavioral changes (Figure 2). At 7 mm, shortly before the onset of schooling, the lens retractor muscle becomes functional, increasing visual accommodation (O'Connell 1981). At 10 mm the swim bladder is inflated for the first time at the water surface; larvae begin nightly migrations to the water surface (Hunter and Sanchez 1976); and the first rods appear in the retina. Over the interval in which schooling begins (12-15 mm) the number of rods increases, perhaps improving peripheral vision; the red muscle deepens from a superficial layer to 2-3 layers deep; and the larva changes from a cutaneous respirator to a gill respirator (O'Connell 1981). In addition, by the time they reach 15 mm larvae have passed a transitory hydrodynamic regime where water viscosity has an important effect on swimming performance, and entered one in which performance is independent of viscosity effects, thus permitting maximum efficiency in the beat-and-glide swimming characteristic of anchovy (Weihs 1980). All organ systems continue maturing throughout the larval phase, but the above circumstantial evidence indicates that onset may be tied to changes related to locomotor efficiency (metabolism and swimming kinetics) and improvements in the visual system.

Although structural developments may set the stage for the onset of schooling, the actual initiation may be triggered by environmental events. In the laboratory, schooling seemed to be triggered by various disturbances such as changing the tank water, cleaning the tank, or other fright-inducing stimuli. In the sea the appearance of predators or perhaps initiation of diel vertical movements to the sea surface could be triggering mechanisms. Such disturbances could act as a trigger only after the larvae reach the appropriate age for onset of schooling.

Hewitt (1981a and b) measured the mean patchiness of the eggs and larvae of northern anchovy taken in ichthyoplankton surveys over the years 1951-79 (6,000+ samples) using Lloyd's (1967) index of

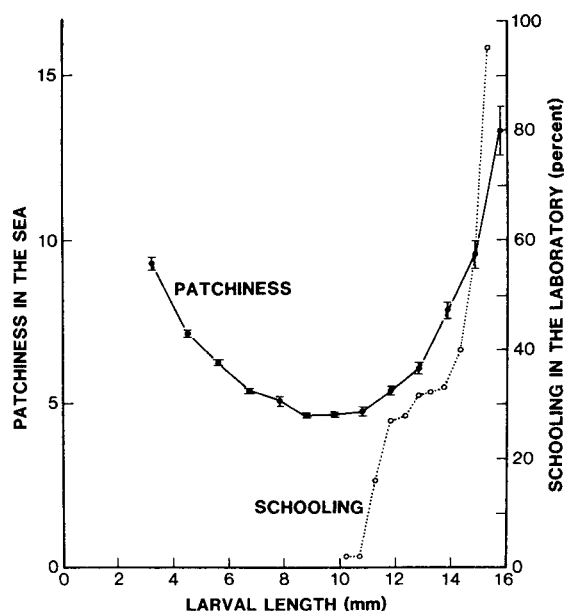


Figure 3. Patchiness of larval anchovy in the sea as a function of larval length (from Hewitt 1981b) and the onset of schooling in the laboratory. Patchiness (solid line), measured by Lloyd's (1967) index, is a measure of the degree of departure of larval spatial distributions in the sea from random dispersion; bars are two standard errors for the index of patchiness. The onset of schooling in the laboratory (dotted line) is measured by the mean percentage of the observation time that larvae were parallel and swimming one body length apart; points are the mean for three laboratory groups combined by length classes.

patchiness. He showed that initially anchovy eggs are quite patchy in the sea, as could be expected from the schooling habits of the parents. After spawning, however, a gradual process of dispersion begins; eggs and, subsequently, larvae become more and more dispersed until the larvae reach about 10 mm (20 days old), whereupon this trend is reversed, and larvae become increasingly more patchy with larval size or age. We have reproduced Hewitt's (1981b) data and plotted on Figure 3 the average schooling index for the data given in Table 1. The increase in patchiness with larval length in the sea closely matches the onset of schooling averaged for the three groups. Thus as Hewitt (1981a) suggested, the change in patchiness—a statistical property of the spatial distribution of larvae—is an effective measure of the onset of schooling in the sea.

A salient feature of larval anchovy schools in the laboratory was that they were dispersed before the daily additions of food, and schooling was not obvious until the larvae had fed. Schools of juvenile jack mackerel also are less cohesive before feeding (Hunter 1966). The restriction of our measurements to post-feeding groups was appropriate for a threshold esti-

mation, but it did mask the fact that the time spent in organized cohesive schools increases throughout the anchovy's larval and juvenile periods (van Olst and Hunter 1970). This gradual increase in the time spent in schools may be related to the maturation of the digestive and feeding systems, which occurs in the juvenile period. Maturation of the digestive system, onset of satiation mechanisms, increases in body reserves, and increases in feeding efficiency probably reduce the time required for feeding and food search and consequently permit schooling to continue for longer periods each day. For example, northern anchovy larvae < 10 mm feed throughout the day and do not appear to satiate. On the other hand, adults satiate rapidly when they feed by biting large prey, and consume a full ration in less than an hour. Satiation is not evident when they feed by filtering smaller prey, but this behavior causes little disruption of school organization, whereas biting behavior affects school structure (Leong and O'Connell 1969).

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