steroid response to stress has been described (*7*).

The results of the second experiment establish that the experiences of the mother during her infancy markedly affect the steroid response of her pups. Thus the offspring of handled mothers showed a reduced steroid response to novel conditions when compared to offspring of nonhandled mothers. However, if the offspring are themselves handled, these differences are abolished. These data can be interpreted in either of two ways. First, direct stimulation of the pups is so profound that it overrides the maternal influence. Second, handling the infant results in changed maternal behavioral and physiological processes, and disturbance of the mother as a function of handling the infant tends to counteract the influence of the experience of the mother during her infancy. Work in our laboratory suggests that maternal stress or treatment of the mother with adrenocorticotropic hormone during nursing significantly affects neuroendocrine maturation and later behavior (*8*).

There is sufficient experimental evidence (*9*) to indicate the importance of maternal influences on subsequent performance both in terms of physiological functions and behavior of the offspring.

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Internal Behavior in Fish Schools

Abstract. *Structural changes within fish schools correlate with declines in environmental oxygen. The changes may result from the responses of individual fish to the environmental consequences of group metabolism. Individual behaviors are adaptive to the school in that they tend to maintain stability between school members and their environment.*

During late fall in North America striped mullet, *Mugil cephalus*, form dense reproductive schools and migrate from bays of the Gulf Coast and southern portions of the eastern seaboard into the open sea. Since the mullet are large (20 to 40 cm), often school at the surface, and usually must migrate through passes into the ocean, extended observation of school structure is possible. We have accumulated data on types of schools and their alterations. When viewed from above the schools resemble geometric figures, such as circles, discs, ellipses, triangles, wedges, crescents, and lines. Internal structure is often modified within seconds or minutes, causing school shape to change in a kaleidoscopic fashion. Normally the schools are composed of a large proportion of polarized individuals. Change in school shape may or may not involve disruption of this parallel orientation, but if it does, disruptions are transient or localized within areas of the school. Individual members of a school continually exchange positions through slight alterations of swimming speed or direction even if school shape is not altered. Similar behaviors have been noted in other schooling species (see *1–5*).

Several factors may cause school structure to change. Nonenvironmental factors, such as variation in individual tendencies to associate or disassociate, could result in the described group behaviors. The importance of these and other innate tendencies are difficult to assess. Environmental factors that might operate include temperature, light, salinity, water currents and waves, predation, feeding, bottom topography, and water chemistry. Of these factors we believe that levels of temperature, light, salinity, and water movement are too homogeneous in marine environments to be responsible for the continuous changes observed in behavior. School structure changes in response to acute predation but it is usually recognizable as a radiating eruption of portions of the school from the water surface (*2*). It bears no resemblance to the slower and continuous modifications of school structure described here. The constant shifting in position of individuals within mullet schools, however, could function in feeding. Positional shifts would place fish in a forward and, presumably, a favorable position for feeding even if the position were maintained for only short periods. But it seems unlikely that all of the school shapes and transitions observed can be solely ascribed to feeding behavior. Examination of the stomach contents of 20 mullet taken from migrating schools in November 1966 revealed that these fish had not been actively feeding for some time before being caught. In general, striped mullet feed in loosely associated groups and not just before spawning (*3*).

The most obvious chemical factors that may be involved include soluble gases and dissolved organic substances of inter- or intraspecific origin. Of these factors only respiratory gases (oxygen and carbon dioxide), dissolved substances such as organic wastes, and perhaps specific organic secretions (pheromones) of intraspecific origin seem likely candidates. Only the respiratory gases, however, can be easily and rapidly analyzed in the field.

If we assume that respiratory gases may effect certain changes or characteristic "postures" in school structure, then the following sequence of events may take place. Reduction of dissolved oxygen and increase of carbon dioxide from school metabolism may be sensed by individual fish. This detection of altered environmental-gas concentration could induce modified behaviors such as changes in direction (orientation), spacing, and swimming velocity. The overall result would be the observed tendency toward continuous variability in group behavior. This hypothesis implies that individual physiological and behavioral response is transferred into social behavior in such a manner that it shortens the exposure of individual fish to less favorable conditions (low oxygen, high carbon dioxide and low pH, or both). In-

Table 1. The effect of size on the reduction of environmental oxygen in schools of striped mullet. The observations were made over an 8-year period.

School	Longest dimension (m)	O_2 (mg/liter)		Oxygen reduction (%)
		Outside	Inside	
		Small schools		
a*	4	6.80	6.50	4.4
b	7	7.20	6.95	3.5
c	9	7.20	7.08	1.7
d	4	7.60	7.20	5.3
		Medium schools		
e*	18	7.12	6.36	10.7
f	15	7.70	6.90	10.4
g	30	7.40	6.85	7.4
h	30	7.00	6.50	7.2
		Large schools		
i†	150	7.30	5.20	28.8
j†	75	7.70	7.00	9.1
k†	240	8.00	6.70	16.3
l	300	7.60	6.00	21.0

* Winkler procedure. All other values by oxygen electrode. † *p*H measured. No difference detectable inside schools with the exception of j.

dividual responses would function to distribute or average the effects of group metabolism to all members of the school. According to this metabolic model of the fish school, gradients of respiratory gases should exist in the water with increased changes associated with increased size and with increased density of schools.

To demonstrate these gradients we measured oxygen and *p*H both outside and inside migrating mullet schools. Specific procedures for oxygen included collection of water samples followed by standard Winkler analysis or, more commonly, the use of a portable oxygen electrode floated through a school. The latter method provided a continuous record which could be correlated with internal school behavior. The Winkler method was less versatile but did allow direct determination of oxygen. The *p*H of the water was measured with a portable meter, the electrode being floated through the school (*6*).

The metabolic effect of a variety of different types of striped mullet schools expressed as the percent reduction of environmental oxygen is presented in Table 1. Reduction of environmental oxygen was detectable within all schools and correlates with school size, large schools producing greater reductions. Although a reduction in oxygen perhaps should be expected, its magnitude and its gross correlation with school size are surprising.

The effect of metabolic carbon dioxide on the environment is far less dramatic than the effect of oxygen, due to the high buffer capacity of sea water. In all instances where *p*H was measured, changes were not detectable, except for one large school measured on 20 November 1965 (j, Table 1). The *p*H decline did not exceed 0.02 units and was, in fact, only detectable as a definite and reproducible downward deflection of the meter needle upon entry into the school. We have calculated a theoretical *p*H decline based on the environmental oxygen reduction of 9.1 percent and an assumed average respiratory quotient of 0.8 for a school of mullet. The expected environmental *p*H decline was obtained from a direct carbon dioxide titration procedure which relates *p*H decline to carbon dioxide added (*7*). The calculation yields an expected change of 0.025 *p*H units, a value in excellent agreement with our field measurements. It is unusual, therefore, that slightly greater *p*H changes were not detected within the larger schools of mullet where oxygen reductions were higher (i and k, Table 1), but this may have been due to the limitations of our equipment. Our results do reveal, however, that sea water is an effective buffer for the amounts of carbon dioxide actually produced by a dense school of mullet.

It is possible to ascribe many of the observable changes in schools and even specific types of structures (varied shapes, spacing, and the like) to the effect of school metabolism. These behaviors may be adaptive in that they lessen the metabolic impact of the school on individual members of the group. However, it is difficult to demonstrate that the intensity of school metabolism is actually sufficient to modify school structure. Demonstrations of exactly how group metabolism might affect structure is even more difficult. And, even if a given school shape, spacing among fish, or a change in structure lessened the effects of group metabolism on individuals, the behavior could result from nonmetabolic as well as metabolic causes. In this case a direct correlation between metabolism and structure could not be demonstrated since a direct cause and effect relationship would not exist.

Our field data provide positive correlation between oxygen gradients within schools and drastic modifications in

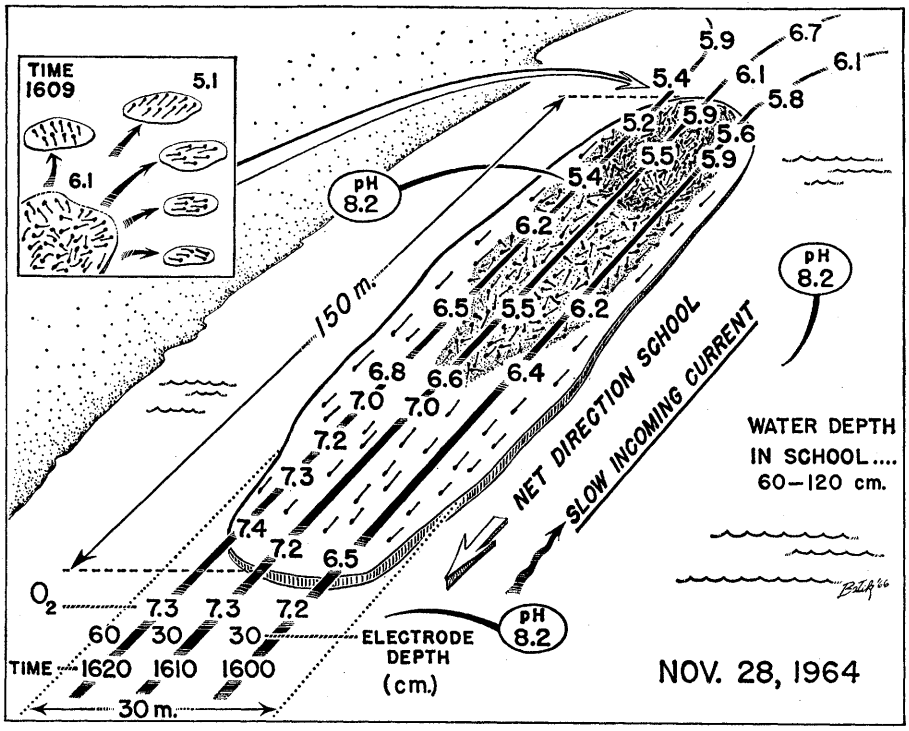

Fig. 1. The relation of school structure and behavior to metabolic modification of environmental oxygen and *p*H. The dot (head) and line (body) signify the orientation of individual fish in various parts of the school. Fish were dense throughout the school, but greatest density occurred in the rear, as indicated by stippling. Fish in the back of the school were actively roiling the water surface. The inset indicates breakup of the rear portion of the school into individual groups. Oxygen reported in milligrams per liter.

school structure. The most dramatic example is represented in Fig. 1. Fish in the front half and along the sides of the school were dense and highly polarized. Toward the center the fish were less polarized and swam slowly in various directions. In the back one-third of the school the fish were extremely dense, often in actual contact, completely unpolarized, and actively roiling the surface of the water. Individual fish appeared to rise to the surface and then retreat below. This activity constantly mixed the entire rear of the school, producing a turnover in the position of its members. Oxygen reductions of 22.6, 24.7, and 28.8 percent were obtained from three traverses through the school. In each instance the oxygen declined abruptly rather than gradually from the front to the back of the school. When we had completed the first oxygen profile and while the electrode was still at the back of the school, an unusual event took place. The entire rear portion of the school broke into several small schools and swam off in several directions (see inset, Fig. 1). While most of these small schools rejoined the large school during the next few minutes, at least one group did not. We conclude that the disruption of school behavior resulted from the abrupt and severe metabolic reduction of environmental oxygen and also an increase in the amount of carbon dioxide or, at least, from some undetected consequence of this metabolism [possibly release of a substance akin to "schrechtstoff" (*8*)]. Avoidance of low oxygen has been demonstrated, however, for a number of species of fish (*9*). Field tests reveal that schooling alewives (*Alosa pseudoharengus*), when presented with a choice, consistently enter water with the least free carbon dioxide, if the difference presented exceeds 0.3 part per million (*10*). While these results do not conclusively demonstrate that the behavior of fish can be influenced by reasonably small gradients of respiratory gas concentrations, the results are consistent with our hypothesis. Not all structural changes in the school can be expected to result from group metabolic effects. For example, the constant slow interchange of position between individual fish in mullet schools is probably not caused by the effects of group metabolism, although metabolic effects may enhance the rate of interchange. That the interchanges are not the result of group metabolism is shown by the experimental demonstration that isolated schooling fish alter position relative to a moving visual field even though orientation to general movement of the field is maintained (*5*). This seems to represent an innate optomotor response which may be species specific. One functional result of this type of behavior is school turnover or mixing. We consider interchange adaptive, perhaps preadaptive to the formation of large dense schools, in the sense that it acts to equalize the time of exposure of each member of a school to the full metabolic impact of the group.

Whether the hypothesis may be generalized to other species must be demonstrated. It seems reasonable to expect, however, that dense schooling species as represented by many herrings and anchovies must change environmental gases through group metabolism. It is important in this regard that the hypothesis suggested here was first formulated from our limited observations of the behavior of small schools of the northern anchovy, *Engraulis mordax*, and not from our study of striped mullet.

Position within a school can expose a fish to a considerable reduction in oxygen. This condition can alter the physiology and behavior of a fish so that its chance for survival, relative to other members of the school, may be diminished if corrective action is not taken.

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Aucuba Strain of Tobacco Mosaic Virus: An Unusual Aggregate

Plant and animal viruses are particulate and, being uniform in size and shape within a given strain, have the capacity to form aggregates of surprising size and symmetry. Many of the spherical viruses aggregate in large and regular crystals with cubic symmetry (*1*). Particles of the common tobacco mosaic virus (TMV) are rod-shaped (15 by 300 mμ) and form several types of inclusions in the cells of host plants (*2*). Some of these, such as the large hexagonal inclusions visible in infected epidermal cells under the light microscope, are truly crystalline and show a repetition of identical units in a regular three-dimensional hexagonal lattice. Others, such as the needle "crystals" and the longer spike- or spindle-like bodies, are paracrystalline. In the latter, virus particles lie parallel to the long axis of the inclusion and exhibit only two-dimensional symmetry (*3*).

During experimentation with the aucuba mosaic virus (*4*), which has particle size and shape similar to the common tobacco mosaic virus and is believed to be a strain of the latter, an unusual type of aggregate was observed. The cover illustration is an electron micrograph (× 44,000) of a thin section of a strip from an infected leaf of Turkish tobacco (*Nicotiana tabacum* L.) killed in an osmium tetroxide solution. The cross-hatched figures which appear in the micrograph are cross sections of aggregates of virus particles that extend well above and below the plane of section. In longitudinal section, the aggregates are elongate and are crossed by parallel dark lines and rows of dots, believed to represent the individual particles cut at different angles. These figures are interpreted to indicate that the aucuba aggregates are made up of layers of 12 to 16 parallel virus particles, one layer placed over another at an angle of approximately 60°, giving the three-dimensional cross-hatching observed. The ends of the particles often project from the sides of the aggregates—as fibers being used to weave a basket