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Problems and Prospects of Studying Schooling Behavior of Fish

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Abstract—The problems and prospects of studying schooling behavior of fish have been considered. Areas that remain little developed or have controversial and contradictory results have been noted: the hydrodynamics and energetics of fish swimming in a school, the mechanisms of fish interaction and the dissemination of information within a school, the principles of forming a coordinated school response to external stimuli and the rapid decay of the reaction, interaction between different schools during their collision or when being part of large aggregations of many schools, patterns of rapid change in the forms of a school. It has been shown that there are no clear ideas about the formation of mechanisms in the ontogeny of fish that underlie coordinated schooling behavior. The sensory base of schooling behavior requires further study. The origin and evolution of schooling behavior and the formation of emergent properties of a school based on individual actions of fish remain at the level of assumptions and hypotheses. The interspecies differences in the schooling behavior of fish, the interaction of schooling fish with fishing gear and adaptation to them are poorly studied. Attention has been drawn to the need for verification in nature of information obtained in laboratory conditions and on aquarium fish that have undergone selection. The necessity of using new technologies, devices, methods of mathematical modeling and other approaches for the intensification of experimental research has been emphasized. Knowledge of the schooling behavior of fish is important for elucidating the general patterns of social behavior of large associations of animals. The development of research is hampered by the lack of generally accepted terminology and quantitative criteria for schooling behavior, which would make it possible to adequately assess, compare, and analyze it. An exhaustive definition of a fish school has been given.

Keywords: fish, schooling behavior, prospects for research, problems, tasks and directions of research, terminology

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Schooling is the most important adaptation that manifests itself at the supraorganismal level and expands the arsenal of means that ensure the successful existence of fish. Despite the fact that schooling as an evolutionary acquisition arose independently in many groups of teleost fish, it has similar properties in different species. Such common, universal properties undoubtedly include a high level of phenotypic uniformity of fish in schools. Schools of fish are also characterized by the behavioral homogeneity of individuals, their equipotentiality. The absence of permanent leaders in schools, especially in large ones, ensures that a school accepts a quick and adequate response to external stimuli that can come from a variety of, often unexpected, directions in the three-dimensional space in which most fish reside. A distinctive feature of schools of fish is their great lability, which manifests itself not only in rapid changes in the external shape of schools, i.e., in the continuity of schooling behavior, but also in changes in the composition of schools, in the breakup of the school and the formation of new schools, in the exchange of fish between schools, their transition from one school to another, subject to the phenotypic similarity of individuals. Due to the lability of the composition of a school, the individual experience of fish quickly spreads and is summed up in the form of the so-called pool of conditioned reflexes of the school. The schooling reflex—the desire to unite with phenotypically similar fish, is a species property that is rigidly fixed genetically and is formed in the ontogeny of fish, regardless of environmental factors. The age at which juveniles begin to show schooling behavior does not correlate with the schooling of adults. In many fish species, only juveniles show schooling behavior, while older individuals lead a solitary lifestyle. An innate property is also a well-pronounced ability in schooling fish to imitate behavior, to manifest an optomotor reaction and rheoreaction.

Schooling behavior is inherent in many fish species (Pitcher, 2001). All of them are united by one common feature of ecology that manifests itself to a greater or lesser extent—an attraction to biotopes in which visual landmarks are either absent or their number is small.

In fish, especially those with facultative schooling, there is a clear tendency to schooling behavior in a homogeneous space, while in an environment saturated with visual landmarks, such fish prefer to stay independent of each other. In all schooling fish, there is a clearly pronounced monomodality in the sensory base of schooling behavior. The significance of visual reception in schooling behavior is exceptionally great; the real participation of other distant senses (lateral line, olfaction, hearing, electroreception) is minimal or not confirmed by rigorous experimental data.

Schooling of fish as a biological phenomenon has been known for a long time, however, schooling became the object of special studies relatively recently, at the beginning of the 20th century, after the publication of the well-known paper by Parr (1927) "A contribution to the theoretical analyzes of the schooling behavior of fishes." Long-term restraint of research in this area is due to the fact that schools of fish in natural reservoirs are a very difficult object for study. The development of hydroacoustic and underwater observation techniques, the widespread use of aerial photography and direct observations of schools of commercial fish from aircraft, the development of experimental studies in artificial conditions, the use of high-speed and high-resolution film and video recording and video image analysis methods, the introduction of quantitative methods for evaluating behavior has made it possible within a relatively short time to significantly expand our understanding of the regularities, mechanisms, and features of schooling behavior of fish (Miller and Gerlai, 2007; Gautrais et al., 2008; Makris et al., 2009; Faucher et al., 2010; Herbert-Read et al., 2011, 2013; Katz et al., 2011; Ward et al., 2011; Marras et al., 2012, 2015; Martignac et al., 2014; Sadoul et al., 2014). Very promising are still the first, but rapidly progressing attempts to introduce into experimental practice biorobot fish that imitate the behavior of fish and are able to drag them along and cause imitative and other schooling reactions. Such biorobot fish, including those with the possibility of feedback, have already been created, for example, for the guppy *Poecilia reticulata*, the zebrafish *Danio rerio*, the three-spined stickleback *Gasterosteus aculeatus*, the eastern mosquitofish *Gambusia holbrooki*, the neon tetra *Paracheirodon innesi*, and some others (Faria et al., 2010; Marras and Porfiri, 2012; Swain et al., 2012; Abaid et al., 2013; Butail et al., 2013, 2014; Polverino and Porfiri, 2013a, 2013b; Phamduy et al., 2014; Landgraf et al., 2016; Bierbach et al., 2020; Romano and Stefanini, 2021, 2022). No less promising may be the method of optical simulation of the presence of a moving object or a group of objects in water with controlled characteristics of their movements (Ioannou et al., 2012; Romey, 2012).

The intensity of the study of schooling of fish, a multifaceted and multilevel ecological phenomenon, is not decreasing. This is due to the fact that the development of such a complex problem is important not only for clarifying general and particular issues of biology and ecology of fish, their behavior, relationships with other representatives of aquatic ecosystems, but also for formulating fundamental, general biological statements about the origin, ways and patterns of development of biosociality. In this regard, it is promising to consider schools of fish as one of the manifestations of planar (equipotential) network structures of living organisms (Krause and Ruxton, 2002; Croft et al., 2005; Oleskin, 2013; Wilson et al., 2014).

However, as in any developing scientific field, the solution of some problems inevitably leads to the emergence of many new questions, while some basic aspects still remain insufficiently studied or contradictory. In schooling behavior, these include the hydrodynamics and energetics of schooling swimming of fish, the mechanisms of interaction between individuals and the dissemination of information within a school, the basic principles for the formation of a coordinated school response to an external stimulus or the rapid attenuation of the response and the refusal of a school to respond, the interaction between different schools when they collide or when being part of large aggregations of schools. There are no clear ideas about the patterns underlying the assortativeness and exterior unification of fish in schools. The formation in fish ontogeny of the mechanisms underlying coordinated schooling behavior and the ability of individuals to show coordinated reactions has not been elucidated. Detailed studies are required to understand the characteristics of the transition of early juveniles from a non-schooling to a group, and then to a schooling lifestyle; the key and limiting factors of this process have not been elucidated. More attention should be paid to the processes of natural disintegration and formation of schools, which occur with a daily cycle, and the behavior of schooling fish outside the "schooling" period, especially in marine fish of the open pelagic zone.

A predominantly qualitative description of schools of fish and the absence of clear criteria for schooling behavior that would make it possible to adequately assess, compare, and analyze it have a great restraining effect on the development of research (Delcourt and Poncin, 2012). Undoubtedly, the problem of the participation and importance of other sensory systems, except for vision, in providing schooling reactions, primarily the lateral line, requires further study. Questions related to the origin and evolution of schooling behavior in the general context of the development of biosociality in animals remain at the level of assumptions and hypotheses. Until now, there are no clear ideas about the presence of schooling in cartilaginous fish (Chondrichthyes). The accumulated large amount of knowledge is insufficient to understand how and to what extent the individual actions of fish lead to the formation of emergent properties inherent in the school and the species as a whole, but absent in the individuals forming the school, what is the evolu-

tionary path for the emergence of these supra-individual qualities (Parrish and Edelstein-Keshet, 1999; Parrish et al., 2002; Ioannou, 2017). To characterize the prevalence of schooling behavior among fish, we still use estimates from almost half a century ago (Shaw, 1978).

Existing knowledge about interspecies differences in schooling behavior of fish is obviously insufficient. Whether and to what extent the species specificity of schooling manifestations and mechanisms exists, whether it is possible to distinguish between schools of different fish species or different populations of the same species, relying on the external characteristics of schools or on schooling reactions—these questions are still far from being resolved (Dagorn and Holland, 2003; Brehmer et al., 2007; Soria et al., 2007; Wark et al., 2011; Rousseau et al., 2022). It is required to check to what extent the features of schooling behavior identified in laboratory experiments are confirmed in the behavior of schools in natural reservoirs. Verification of information obtained in the laboratory is especially important and interesting for large schools and mega-schools of marine pelagic fish (Krause et al., 2000; Rieucau et al., 2015; Ward et al., 2020).

Some caution should be exercised in dealing with the results obtained on aquarium fish and fish raised in artificial conditions for many generations. Long-term cultivation and selection of fish and, as a result, domestication, can change or even distort the manifestation of a genetically fixed schooling reflex. To what extent this behavior can be disturbed by domestication and selection is not clear (Ruzzante and Doyle, 1993; Ruzzante, 1994).

New interesting directions are emerging, the development of which can lead to obtaining information about previously unknown features of the manifestation of schooling reactions and intra-school interactions by fish. For example, studies have already begun on the manifestation of lateralization of swimming by schooling fish—the tendency of fish to turn around an obstacle, mainly to the left or right. It turned out that the schooling coral fish, yellow-tail fusilier *Caesio teres*, which normally avoids obstacles more often on the right, increases the tendency to "right-sidedness" when danger arises (Chivers et al., 2016). In the population of this species and many other animals, the proportion of individuals using the opposite tactics usually reaches 10–35% (Vallortigara and Rogers, 2005). It is important that among the 16 fish species studied, lateralization is characteristic of all schooling species without exception and only 40% of fish that do not belong to the schooling fish (Bisazza et al., 2000). The adaptive meaning of the presence of such individuals in schools of fish, one of the characteristic features of which is the high phenotypic uniformity of the individuals that form them, has not yet been disclosed. No less interesting, but extremely poorly studied, are the ideas about the preservation by fish uniting in a school of their individual characteristics and qualities, i.e., to what extent personalization can manifest itself in schools (Jolles et al., 2019; Tang and Fu, 2020; Ward et al., 2020).

It is also alarming that studies to elucidate the patterns and mechanisms of intra-school interactions and other basic problems of schooling behavior are carried out on fish species that are difficult to attribute to typical or highly schooling species, for example, on guppies, mosquitofish and other Poeciliidae, three-spined stickleback, goldfish *Carassius auratus* and some others. These fish are convenient as model objects for various experimental studies, which explains the significant amount of data obtained on their example, especially in recent years. However, the degree of their school unity is low, and they spend most of their daily time budget not on school swimming, but on other forms of behavior, such as feeding or reproduction. Additional substantiation is required to extend findings and conclusions obtained on such species that can be attributed, even then with certain conventions, to facultative schooling fish, to all schooling fish, including obligate schooling fish. The absence of such substantiations creates difficulties and uncertainties in the assessment and interpretation of data obtained on fish, which can be considered true schooling with great limitations. Many researchers inevitably face this problem when comparing their own data or preparing analytical reviews. One assumption that still allows the use of such data may be the concept of a continuum of schooling behavior.

Many unresolved problems concern applied aspects, primarily fisheries. It is known that schooling fish are able to learn to avoid fishing gear, and such skills can quickly spread in traditional fishing areas (Kukhorenko, 1977). Knowledge about the skills that commercial fish develop in relation to fishing gear is not enough. It is not known whether such avoidance habits occur with all fishing gear used or only with some types of gear. There is no information about the ability of fish to learn to avoid modern pelagic trawls, which are so large that they cannot be perceived by fish as a single object. Apparently, learning concerns some separate elements of the trawl, or the acoustic (hearing) or seismosensory and hydrodynamic (lateral line) stimuli generated by it. Studies of the reactions of fish schools to fishing gear can increase the efficiency of fishing and reduce unwanted losses (Graham et al., 2004; Tenningen et al., 2012; Handegard et al., 2017). At the same time, due to their aggregation, schooling fish are easier to detect and catch, which makes them vulnerable to modern fishing. More than half of the commercial fish species are schooling, and many of them are in a depressed state due to overfishing (Pitcher, 1997, 2001; FAO, 2022).

The rapidly developing aquaculture poses its new challenges, such as studying the behavior of fish schools inside large mesh cages or tanks used in mod-

ern aquaculture (Oppedal et al., 2011; Xu and Qin, 2020; Park et al., 2022; Chen et al., 2023). A recent issue is the conformity of modern fisheries and aquaculture technologies with the increasing demands for compliance with bioethical standards in fisheries, in particular the increase in the survival of schooling fish that are undesirable for catching or escaping from fishing gear, the need to create new or modernize existing gear and fishing technologies that cause minimal damage to such individuals and provide conditions for these fish to maintain the school (Handegard et al., 2017; Anders et al., 2019; Torgerson-White and Sánchez-Suárez, 2022).

The compilation of accurate forecasts of the timing and places of formation of exploitable concentrations of schools of fish and the direction of their movements (commercial exploration) remains the problem. This requires not only accurate knowledge of the mechanisms and patterns of schooling behavior, but also many features of the biology of specific objects of fishing, their way of life, the development of the senses, the ability to learn, and the like. To solve the problems of increasing the efficiency of methods of fishing for schooling fish, mathematical models are created, for the development of which a large amount of accumulated factual material and knowledge of the main patterns and mechanisms of schooling behavior are used. Such models are being used not only to predict the reactions of schooling fish to various fishing gear under various conditions, but also to qualitatively describe the typical manifestations of the movements of an entire school as a whole and the movements of individuals, to verify and refine already known patterns and to search for new mechanisms within and inter-school interactions (Buyakas et al., 1978; Niwa, 1994; Nonacs et al., 1998; Gunji et al., 1999; Couzin et al., 2002; Huse et al., 2002; Kunz and Hemelrijk, 2003; Viscido et al., 2004; Hensor et al., 2005; Zheng et al., 2005; Gautrais et al., 2008; Hemelrijk and Hildenbrandt, 2008; Abaid and Porfiri, 2010; Beyer et al., 2010; Mayer, 2010; Lopez et al., 2012; Hemelrijk et al., 2015; Herbert-Read et al., 2015; Watts et al., 2017; Oza et al., 2019; Jhawar et al., 2020; Wang et al., 2022; Ceron et al., 2023; Gómez-Nava et al., 2023).

Of great interest is the search and elucidation of the general and specific features and mechanisms of schooling behavior of fish and the behavior of other animals, vertebrates and invertebrates, uniting in a swarm (insects), a flock (birds), a herd, a drove, a crowd, and the like (MacGregor et al., 2020; Burford et al., 2022). But such a comparative analysis is impossible without close cooperation between researchers of the behavior of different groups of animals. Using the example of fish, non-standard problems of reversible transitions of animals from coordinated behavior in associations, such as schools, to disorganized crowd behavior are beginning to be elucidated (Larrieu et al., 2022).

The continuing terminological confusion, which, unfortunately, has not yet been overcome, has a serious restraining effect on the further development of research. As a result, many of the works performed either cannot be used at all for a comparative analysis of schooling behavior and the formulation of generalizations, or the use of such materials should be extremely careful. In some cases, this problem remains unsolvable. The address of the participants of the International Conference on Fish Behavior, held about half a century ago in Bergen in 1967, was to call on the authors to indicate what specific meaning they put into the concept of a school. This call remains relevant today. As before, the assignment of the observed behavior of fish to schooling or group shoaling in many cases, unfortunately, occurs heuristically, i.e., based on the researcher's own ideas and accumulated personal experience (Delcourt and Poncin, 2012). Such a feature as the parallel orientation of fish in schools cannot be attributed to an obligatory feature of schooling behavior, which is inherent in schools all the time. There are a large number of examples showing that the polarization of fish in a school does not manifest itself in all situations, it is absent when a school is resting, or when fish are feeding, during defense (a school of all-round visibility), and so on. At the same time, a strictly unified arrangement of fish may not be related to schooling, as is the case with sharks. In our opinion, the behavior of fish observed in the experiment or in nature can be classified as schooling only if it meets the basic and mandatory requirement—association of equipotential fish showing coordination of actions. The maintenance of a parallel orientation by fish when swimming is in most cases a sufficient, but not a necessary condition for classifying the locomotor activity shown by fish as a schooling type of behavior.

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

CONFLICT OF INTEREST

The author of this work declares that he has no conflicts of interest.

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