Size, Shape, Numbers and Composition of Fish Schools

A. O. Kasumyan[a], * and D. S. Pavlov[b]

[a] *Lomonosov Moscow State University, Moscow, Russia*

[b] *Severtsov Institute of Problems of Ecology and Evolution, Russian Academy of Science (IPEE RAS), Moscow, Russia*

*e-mail: alex_kasumyan@mail.ru

Abstract—Data on the size and shape of fish schools, number, size, and species composition of individuals included in them have been considered. The largest schools, numbering up to hundreds of thousands of individuals or more, are formed by mass marine pelagic fish. The shape of fish schools of the same species is extremely diverse and changes rapidly, depending on the age and size of the fish, their mobility, condition, and other features. The classification of schools has been given—migrating (polarized), feeding, spherical (globular) and others. Schools can become denser or sparse, change the depth of swimming, break up and joint with neighboring ones. The variability of the linear sizes of fish schools and the number of individuals included in them reflects the high plasticity of schooling behavior and its susceptibility to the influence of various factors. Schools are characterized by high homogeneity of the species and size composition of fish and the absence of individual differences in fish. In some cases, schools may consist predominantly of female or male fish. Uniformity is the most important characteristic of fish schools and indicates assortativeness when fish unite into schools. The greatest homogeneity is characteristic of migrating schools of pelagic fish. Multispecies schools are most often formed by juvenile fish.

SIZES OF SCHOOLS

Fish schools are bulk structures, i.e., three-dimensional formations (Partridge, 1980). Therefore, the external parameters of schools should be estimated not only by length and width, but also by height. The sizes of schools vary extremely strongly; in the same observation period, fish of the same species form schools, the parameters of which differ tens and hundreds of times. For example, the extent (length) of moving schools of the Black Sea horse mackerel *Trachurus mediterraneus ponticus* varies from several meters to several hundred meters (Tikhonov, 1958).

The schools largest in size are formed by marine pelagic mass fish. To estimate the size of schools, hydroacoustic methods are used, as well as methods of photographic recording and visual observation, including from aircraft and drones. With the use of such methods, it has been established that the schools of the chub mackerel *Scomber japonicus* reach 100–150 m in length and 15 m in width (Hara, 1985a, 1985b). Schools of the splendid alfonsino *Beryx splendens* (Berycidae) are several hundred meters long (300–1000 m) and up to 30–90 m high (Galaktionov, 1984). Schools of the Atlantic herring *Clupea harengus* during the feeding period in the open sea reach 50 m in length with an average height of ~3 m (Tokarev,

1958). Their average area is (according to data for 44 different schools) ~ 1000 m^2 (Nøttestad et al., 2002), the area of some of the herring schools exceeds 3000 m^2 (Misund et al., 1995). Schools of the European anchovy *Engraulis encrasicolus* have a length of 20–1600 m at a height of 8–60 m (Tokarev, 1953), while the area of individual schools (flocks) of anchovy during wintering near the northern shores of the Black Sea exceeds 200000–400000 m^2, and the volume they occupy reaches several million cubic meters (Table 1) (Berenbeim, 1955). The mean school diameter of the northern anchovy *E. mordax* off the Pacific coast of North America is 29.1 m, but about half of all fish (by biomass) are concentrated in schools > 70 m in diameter (Smith, 1981). The volume of some schools of the roundnose grenadier *Coryphaenoides rupestris* can exceed 1000 m^3, but does not remain constant and has a certain daily dynamics (Fig. 1) (Galaktionova and Galaktionov, 1990). The area of individual schools of the Black Sea horse mackerel during spring migrations reaches 50000 m^2 (Tikhonov, 1958). Interestingly, the average sizes of schools of marine pelagic fish in three geographically remote fishing areas of the Atlantic Ocean are quite similar, and the frequency distributions of the length, width, and height of the studied schools are also similar (Fig. 2). This indicates the
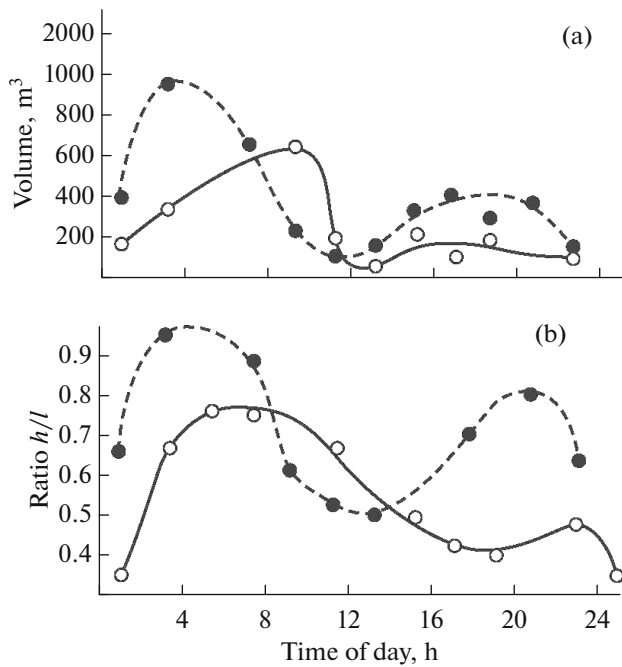
Fig. 1. Diurnal rhythms of changes in the volume (a) and proportions (b) of schools of the roundnose grenadier *Coryphaenoides rupestris* in different seasons of the year: (-○-)—spring, (-●-)—summer; *h*—school heigth, *l*—school length (according to: Galaktionova and Galaktionov, 1990).

universality of the mechanisms leading to the formation of large schools by fish (Paramo et al., 2010). However, it should be borne in mind that the linear dimensions of the same school can quickly, in fact every minute, and in a wide range change due to various reasons—changes in the speed of movement of fish, the appearance of danger or the discovery of food, and the like (Misund et al., 1998).

Often fish schools are located so close to each other that it is not always possible to clearly differentiate them. Moving in one direction, they are constantly splitting into smaller schools, and then again joint among themselves into one single school. During observations from an aircraft, the total length of the chain of closely spaced schools of the golden grey mullet *Chelon auratus* and the leaping mullet *Ch. saliens* migrating along the eastern coast of the Caspian Sea is up to 100 km (Probatov, 1953). In the Volga delta, juvenile bony fish migrating upstream for wintering form a continuous many-kilometer long line in the coastal strip (D.S. Pavlov, own data).

According to estimates made using modern remote methods (OAWRS—ocean acoustic waveguide remote sensing), which allow covering large areas, the length of schools of marine pelagic fish can exceed 10 km and cover an area of tens of square kilometers. Such megaschools consist of tens of millions of individuals and represent the largest associations known in animals (Makris et al., 2006).

SHAPE OF SCHOOLS

A shape that schools of even the same fish species take is extremely varied and rapidly changing (Nøttestad et al., 1996). This is especially noticeable when observing from above: from a height of 400−500 m, fish schools look like brownish and dark spots if the fish are not deeper than 25−30 m from the sea surface. Thus, while moving along the coastline in the Caspian Sea, large schools of mullet (*Mugil* spp.) take on a round or horseshoe shape, a shape of an elongated ribbon, and others (Makarchuk and Belousov, 1953). Large schools of marine pelagic fish, such as the Far Eastern sardine *Sardinops sagax melanosticta*, are characterized by a variety of shapes (Fig. 3). An assessment of shapes of the Atlantic herring schools using sonars in the North Sea (Misund et al., 1995) showed that out of 166 schools, about two thirds were round, oval or close to square in shape, slightly less than a third were elongated to varying degrees in length, in a small number of schools, the shape was assessed as

Table 1. Dimensional characteristics of large flocks of the European anchovy *Engraulis encrasicolus* during wintering in the Black Sea (according to: Berenbeim, 1955)

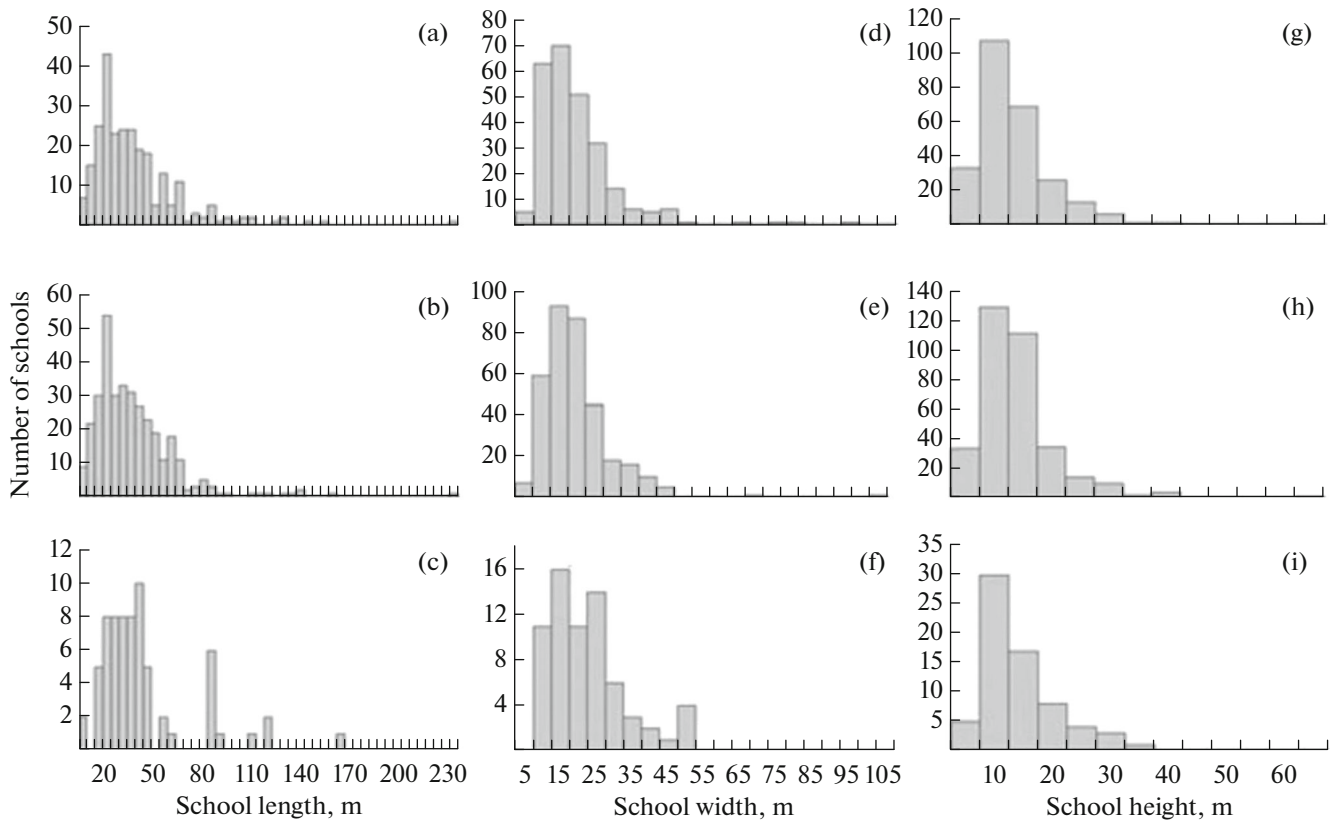| Flock number	Area, thousand m^2	Average height, m	Volume, million m^3
1	129.7	18.4	2.4
2	217.9	14.0	3.1
3	444.4	19.6	8.7
4	171.6	18.0	3.1
5	133.8	17.5	2.3
6	25.7	22.0	0.6
7	3.4	23.5	0.1
8	72.4	18.5	1.3
9	186.7	18.5	3.4
10	390.5	17.2	6.7

Fig. 2. Frequency distribution of length (a–c), width (d–f) and height (g–i) values of pelagic fish schools in three geographically remote fishing areas: a, d, g—off the coast of Mexico in the Gulf of Mexico (257 schools); b, e, h—off the coast of Venezuela in the Caribbean Sea (343 schools); c, f, i—off the coast of Senegal in the Central Atlantic (68 schools). The sizes of schools were estimated using multibeam sonar; the species composition of fish in schools was not determined (according to: Paramo et al., 2010).

Fig. 3. Forms of large schools of the Far Eastern sardine *Sardinops sagax melanosticta* according to observations from an airplane (according to: Kaganovskii, 1939).

parabolic and amorphous (Fig. 4). The rounded or oval shape of the school is associated with an attempt by fish to be less noticeable when danger arises, while elongated or parabolic fish schools usually form when moving or feeding (Pitcher and Partridge, 1979; Partridge et al., 1980).

The schools constantly change their shape and size, become denser or sparse, form "pseudopodia" and "vacuoles", change the swimming depth, split or joint with neighboring ones. According to some estimates made for the Atlantic herring, such transformations occur on average every 15 min, and inter-school
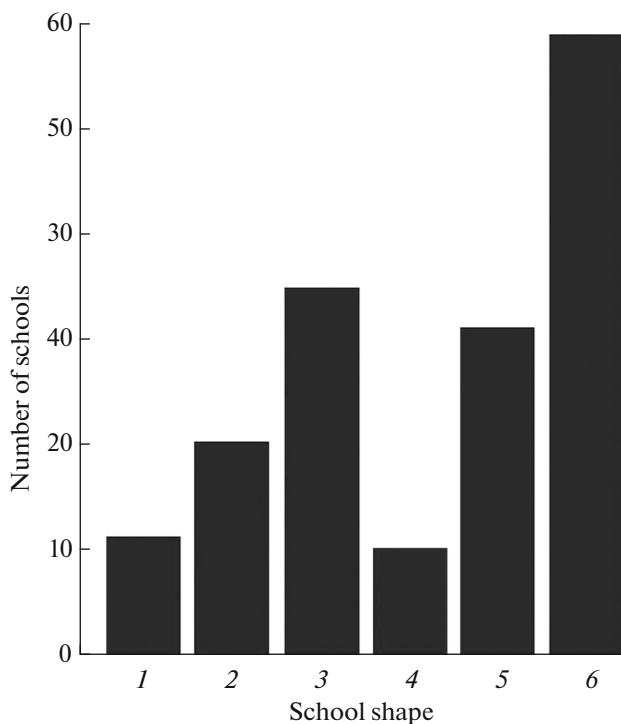
Fig. 4. Frequency of occurrence of schools of different shapes in the Atlantic herring *Clupea harengus* in the North Sea. School shape: *1*—amorphous, *2*—round, *3*—oval, *4*—parabolic, *5*—elongated, *6*—square (according to: Misund et al., 1995).

contacts, i.e., approaches and leaves, joins and splittings are recorded every 23 min (Nøttestad et al., 2002). Another estimate was based on recording the behavior of each of the 14 simultaneously monitored schools for 1 h (Pitcher et al., 1996). According to this estimate, various schooling transformations, including changes in shape, occur at intervals of approximately 5 min. Changes within schools occur about twice as often as changes caused by inter-school interactions or attacks by predatory fish (Fig. 5). Similar values were obtained during sonar observation of schools of the Far Eastern sardine *S. sagax*: changes in the shape of the schools occurred on average every 2.08 min, and the splitting or join of schools occurred every 5 min (Misund et al., 2003). Similar rapid transformations in the shape or abundance are demonstrated by megaschools, large school associations of marine pelagic fish (Makris et al., 2006).

A school takes the most typical external shape during the movement and when they are in the current. They are called *migrating schools*, another name for such schools—*polarized schools*. When viewed from above, they have an elongated or pointed shape (Fig. 6a). A sign of migrating schools is a single, strictly parallel orientation of fish. An important feature of migrating schools is the high coordination of fish movement during migration and complex maneuvers. In general,

due to the constant movement of fish within a school, its outlines are unstable and changeable even over relatively short periods of time (Zuyev and Belyayev, 1970), however, the parallel orientation of individuals and the elongated shape of migrating schools are usually well pronounced.

When the movement of migrating schools slows down and fish switch to feeding, the shape of the school becomes rounded from an elongated one, and its structure changes—the single orientation of individuals is violated, the fish disperse, the school becomes loose. The location and orientation of fish are completely determined by the peculiarities of the feeding behavior of individuals. Such schools are called *feeding schools* (Figs. 6b–6d). Being in them, fish show characteristic foraging behavior. In small planktivorous fish at this time one can see short, sharp and frequent bursts and turns to the sides. The transition from a feeding school to a migrating school and vice versa occurs quickly, for example, when fish move from one feeding place to another, as can be easily seen by observing the behavior of juvenile fish feeding in shallow water (Carvalho et al., 2007). Looking even more loose are *resting schools* (Fig. 6e), in which the fish are inactive and, as it were, hang in the water. Resting schools are clearly visible in summer at the water surface in the middle of the light, hottest period of day, when the feeding intensity of most fish decreases sharply.

When there is a threat of attack by predators or any other danger, schools become less mobile and denser, the fish in them are usually oriented with their heads not inward, but in different directions, therefore such schools are called *schools of all-round visibility*. Many marine pelagic fish, under the direct threat of predation, form a spherical school, often called a *globular school*. A spherical school, as well as a school that maneuvers to avoid an attacking predator, is called *defensive school* (Figs. 6f–6h). The moving activity of frightened fish in such schools, especially in spherical ones, is high; fish quickly move within a school and freeze only for a short time. During rapid movements within such schools, fish located on the periphery move in the same direction. A defensive school is characterized by maximum maneuverability. Its outlines, density, orientation of individuals escaping from the attack of a predator change rapidly, in some cases the integrity of the school is violated when escaping from danger, and it breaks up into two or more smaller schools, which can then again quickly unite into one single school.

If in the European anchovy, the Black Sea horse mackerel, the Atlantic herring, the Atlantic cod *Gadus morhua*, the height of the school can be significant and slightly less than the length or width, then in the schools of the golden grey mullet or the leaping mullet, all fish are located almost in the same plane (Probatov, 1953). Such schools are often called *flat schools*, unlike
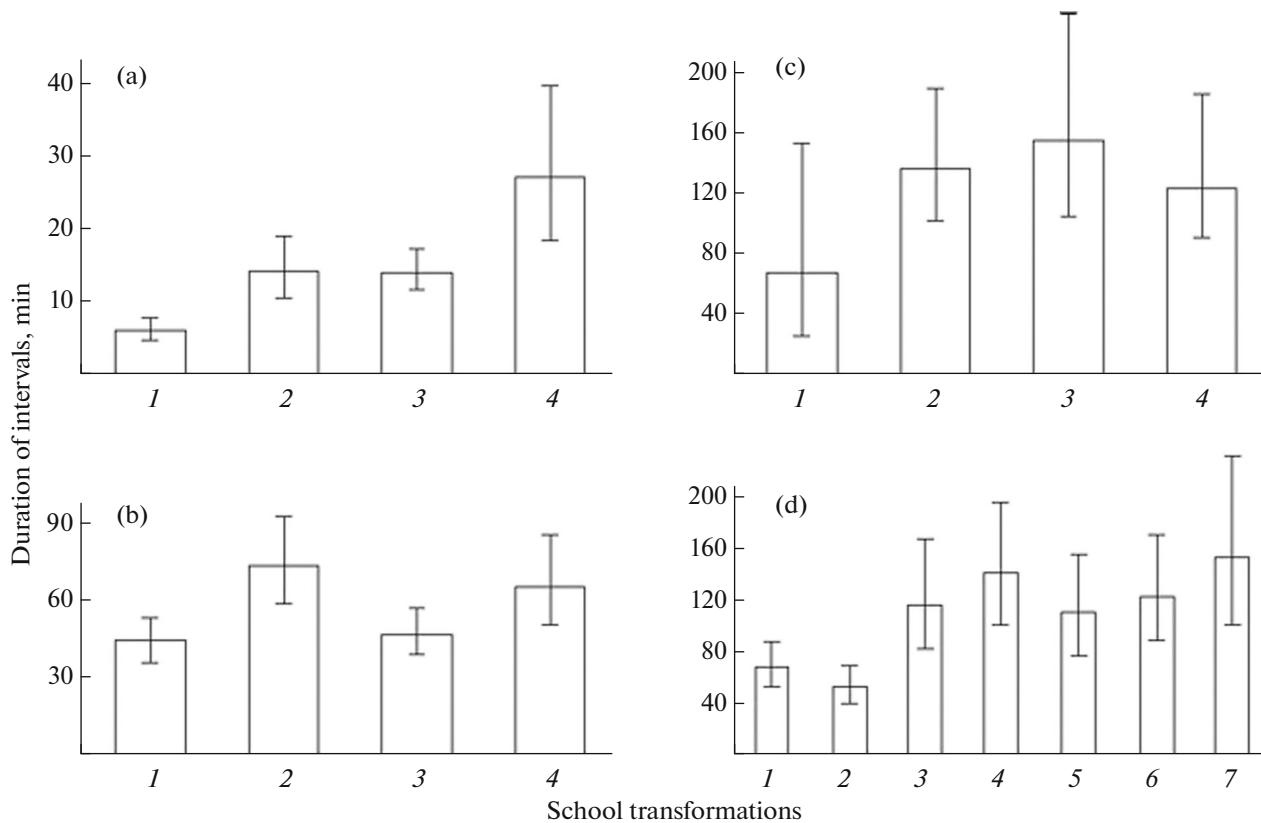
Fig. 5. Frequency distribution of the duration of time intervals between different intra- and interschool transformations occurring within 1 hour in 14 simultaneously observed schools of the Atlantic herring *Clupea harengus*: (a) intervals between school transformations: *1*—all transformations in total, *2*, *3*—intra- and interschool transformations, respectively, *4*—transformations caused by predator attacks; (b) intervals between interschool transformations: *1*—approach, *2*—association (join), *3*—leave, *4*—separation; (c) intervals between transformations caused by predators: *1*—located near a school, *2*—attack by a single predator or a small group of predators, *3*—attack by a school of predators, *4*—predators following or pursuing a herring school; (d) intervals between intra-school transformations: *1*—rapid (1–2 min) increase in density and decrease in the size of a school, *2*—rapid (2–5 min) redistribution of intra-school groupings, *3*—circular movements of fish and the formation of a "vacuole" in the center of a school, *4*—formation of one or several elongated protrusions ("pseudopodia"), *5*—elongation of a school in the direction of movement (length to width ratio of the school > 3 : 1); *6*, *7*—rapid (1 min) drops of a school to a depth (*6*) or ascents to the water surface (*7*); (⊓)—average value, (⊥)—95% confidence interval (according to: Pitcher et al., 1996).

bulk schools, in which the fish are at different levels relative to each other. The goatfish (Mullidae) usually move in flat schools in sandy shallow water (Mochek, 1987). Schools of juveniles of many freshwater fish, staying in the current or moving downstream or upstream, have an insignificant height.

Moving schools of the European anchovy have an elongated shape with a length to width ratio of 2.09 : 1.00 on average (Squire, 1978). A shape of the chub mackerel schools is even more elongated and their length exceeds their width by 6–10 times (Hara, 1985a). A shape of small moving schools of the herring *Harengula* sp. resembles an oblate ellipsoid with an axis ratio of 2.1 : 2.0 : 1.6 (Cullen et al., 1965). A formula approximating the school by an ellipsoid of revolution has been proposed (Galaktionova and Galaktionov, 1990). Since schools are three-dimensional structures, the width of the volume occupied by the school should also be taken into account in order to analyze their spatial characteristics. Schools of the yellow-eyed mullet *Aldrichetta forsteri*, close in shape to an elongated spheroid, have a length–height–width ratio of 5 : 2 : 1 (Middlemiss et al., 2018). Despite the significant variability in the shape of a school of fish, it is generally accepted that, on average, the proportion of its length, width, and height is close to 3 : 2 : 1. It is also assumed that an ellipsoid shape makes a school less noticeable (Pitcher and Partridge, 1979). Using high-precision hydroacoustics methods, it was found that a flattened spheroid-shaped school is typical for fish (Atlantic herring) located near the surface or in the bottom layers of water, while in the water column, a shape of a school is closer to spherical (Misund, 1991—cit. by: Pitcher and Parrish, 1993). The European anchovy during fattening forms round or oval schools (Golenchenko, 1956), and when migrating through the Kerch Strait from the Azov Sea to the Black Sea, the shape of schools is extremely variable
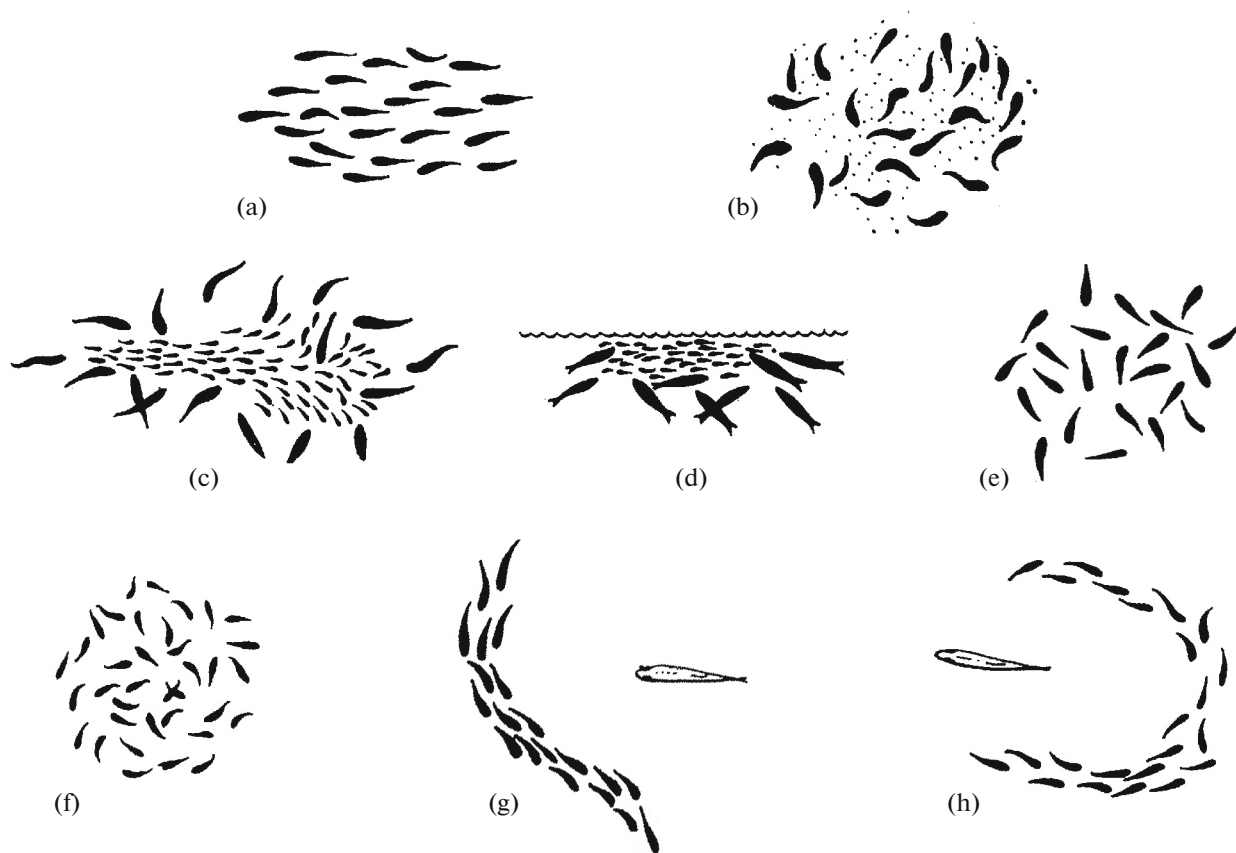
Fig. 6. Main types of fish schools: a—migrating school; b—d—feeding schools of planktophage fish (b) and pelagic predators (c, d—top and side views, respectively); e—resting school, f —defensive school of all-round visibility; g, h—defensive school evading the attack of a single predator (according to: Radakov, 1973, modified).

(Makarchuk and Belousov, 1953; Tokarev, 1958). Such schools with a rapidly changing configuration are called *amoeba-like schools* (Krotov, 1938). The proportions of a school can have a certain diurnal dynamics, from a shape close to spherical in the morning and evening hours (the ratio of the height to the length of a school is 0.8−1.0) to elongated in the daytime (0.5−0.8) (Fig. 1) (Galaktionova and Galaktionov, 1990).

When observing the same school of fish, one can easily see all the transitions from migrating or amoeba-like to feeding or resting, and when a threat arises, from a resting or feeding school to migrating or defensive. Even during rest, when the fish are oriented differently, they do not disperse far from each other and almost instantly re-form a polarized school upon a sudden fright (Rangeley and Kramer, 1995). The diversity of schooling behavior, the rapid transition of a school from one type to another in accordance with the specific life functions of fish—feeding, resting, avoiding danger, migration, etc., indicate the presence of a certain spectrum of forms of schooling behavior that are different in structure and purpose, their unity and mutual reversibility. They form a continuum of forms of schooling behavior, which consists in the

constant and rapid transition of a school from one form to another—from migrating to feeding, from defensive or resting again to migrating school, and the like. The change in the forms of manifestation of schooling behavior does not occur in the course of ontogenetic transformations or seasonal and daily cycles, but constantly and quickly on shorter time scales (seconds, minutes, hours) and, undoubtedly, is the most important feature of this type of fish behavior.

NUMBER OF FISH IN SCHOOLS

The minimum number of fish groups capable of schooling is three individuals (Darkov, 1975; Darkov, 1980; Partridge, 1980; Kanehiro et al., 1985). Usually the number of individuals in fish schools exceeds this minimum level and varies widely, including among representatives of the same species. Large predatory fish often keep in small schools, consisting of only a few individuals. Small schools are typical for juvenile river fish, especially in streams and small rivers. At the same time, during the period of spawning, migration or fattening, many fish gather in large schools, uniting hundreds of thousands or millions of individuals. The

largest schools are formed by many marine pelagic fish.

There is a large body of data illustrating the range of possible numbers of fish in schools. Thus, by targeted catches by commercial trawls of the Atlantic herring schools it was found that the total mass of fish in a school reaches 100 t (Radakov, 1973). Based on the average body weight of herring, the number of individuals in such schools was determined to be 250000 ind. According to other researchers, the number of fish in the Atlantic herring schools varies from 100 individuals to 400 thousand and more (Misund et al., 1995). According to hydroacoustic measurements, in herring schools 100−280 m long and 4−14 m thick, there are 11000−103000 fish in 1 m^3 of the volume occupied by the school (Trevorrow and Claytor, 1998). Similar values have also been obtained for schools of some other marine pelagic fish: in yearlings of the flathead grey mullet *M. cephalus*, schools may consist of more than 300000 individuals (Hellier and Hoese, 1962), in the Far Eastern sardine, the numbers of schools reach 500000 (Kaganovskii, 1939, 1943[1]). Schools of large bluefin tunas *Thunnus thynnus* weighing 100−350 kg range from a few to over 1000 ind. (Lutcavage et al., 2000).

However, in many cases the number of fish in schools, including marine pelagic fish, is much smaller. So, according to visual calculations from the hydrostat, usually schools of the large Atlantic cod include up to 10 individuals, of the smaller cod—up to several tens of individuals, schools of the haddock *Melanogrammus aeglefinus* usually consist of 10−30 fish, of juvenile cod (Gadidae)—of several hundred (Kiselev and Solovyov, 1961); schools of juveniles of the Atlantic silverside *Menidia menidia* 11−12 mm long consist of 30−50 ind. The number of fish in schools of the one-spot snapper *Lutjanus monostigma* does not exceed 1000−2000 (Potts, 1970), in schools of the big-scale sand smelt *Atherina boyeri*—1000, juveniles of the European anchovy—several tens of thousands, juveniles of the Black Sea red mullet *Mullus barbatus ponticus*—200, wrasses of the genus *Symphodus*—up to several dozen (Aronov, 1977). Schools consisting of several dozen individuals are formed by immature individuals of the ocean sunfish *Mola mola* (Abe et al., 2012). Juveniles of the three-spined stickleback *Gasterosteus aculeatus* keep in schools, the number of individuals in which varies from 6−8 to 50 (Peuhkuri and Seppä, 1998), in schools of juveniles of the Eurasian minnow *Phoxinus phoxinus*, there are from several tens to several hundred larvae or juveniles (Soin et al., 1981). Joint schools of juveniles of the golden shiner *Notemigonus crysoleucas*, the banded killifish *Fundulus diaphanus* and some other fish spe-

cies range from 6 to over 750 individuals, with the majority of schools exceeding 20 individuals (Krause et al., 1996a, 1996b, 1998).

Such a pronounced variability in the linear sizes of fish schools and the number of individuals included in them reflects the high plasticity of this form of behavior, its susceptibility to the influence of various internal and external factors. In some cases, the inconsistency of existing information about the size and abundance of fish schools is associated with the ambiguity of the content that different researchers put into the concept of a school. It is not always clear whether they are dealing with one school, or with several at the same time, or they are evaluating the parameters not of a school, but of a cluster of fish in which individuals are not interconnected by a common behavior. The point of view is expressed according to which the huge migratory aggregations of many marine pelagic fish represent a single school, the number of which depends only on the number of individuals ready for migration (Milanovskii and Rekubratskii, 1960). However, such gigantic clusters should be considered as spatial associations or aggregations of many, to some extent, independent schools, between which there may be no connection. It is suggested, based on calculations and modeling, that there is a maximum size of a school, above which it is no longer perceived by the fish entering it as a whole (Kunz and Hemelrijk, 2012).

The numbers of schools of the same fish species may depend on the age and size of the fish, their condition, living environment, and the like. So, if the large Atlantic cod keep in small schools (Kiselev and Solov'ev, 1961), then small individuals of this species and the haddock form schools of up to 2−3 thousand individuals, while with an increase in the size of fish, their number in a school decreases. It has also been noted that schools of these fish in the pelagial are usually more numerous than near the bottom (Konstantinov, 1977) or in the coastal area (Mochek, 1987). In the guppies *Poecilia reticulata*, the relationship between the size of fish and the number of fish in schools is weak (Hoare et al., 2000a), while the presence of a flow affects the number of schools strongly—in the current, the guppies stay in small schools, but in places where there is no current, the schools are much larger (Hockley et al., 2014).

Thus, fish schools are very diverse in size, shape and number of individuals that make them up. The parameters reflecting these external characteristics of schools are very unstable and easily shifted under the influence of various factors and living environment, age or condition of fish, which emphasizes the high plasticity of these characteristics of a school and schooling behavior in general.

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[1] Kaganovskii, A.G., Composition of shoals and behavior of the Far Eastern sardine *Sardinops sagax melanosticta* (Temm and Schleg) in connection with oceanographic conditions, *Doctoral (Biol.) Dissertation*, Sverdlovsk: Moscow State Univ., 1943.

COMPOSITION OF SCHOOLS

In most cases, fish schools are characterized by a high uniformity of species and size composition and the absence of noticeable individual differences in the physiological status of the individuals included in them (Mesyatsev, 1939; Breder, 1951, 1959). Fish in schools have the same maturity of the gonads, a similar level of activity of the sympathoadrenal system (the level of catecholamines in the brain), other physiological parameters also coincide (Radakov, 1973; Nechaev, 1991). In some situations, for example, during the pre-spawning period, fish schools can unite mainly females or males, as is observed in the capelin *Mallotus villosus* (Davoren et al., 2006). The uniformity of individuals in terms of species, size, and internal condition is the most important characteristic of fish schools (Shaw, 1962, 1978; Radakov, 1973; Partridge, 1982; Manteifel', 1987; Pitcher and Parrish, 1993).

Dimensional Composition of Fish in Schools

Fish in schools are similar in size and usually do not differ from each other by more than 50% of the average body length. Such data were obtained mainly for migrating schools of mature fish during their feeding, wintering, or spawning migrations (Shaw, 1962). There are claims that if fish differ in size by more than head length, then this prevents the formation of a single school, and that differences in length limit the formation of common schools to a greater extent than belonging to different species (Schäfer, 1955). An analysis of the size composition of 34 fish schools caught in a small lake showed that the average value of the coefficient of variation in the body length of fish in a school is ~16% (Krause et al., 1996a).

The size and species homogeneity of fish schools in natural water bodies indicates that the association of fish does not occur randomly, and that the high assortativeness (non-randomness) of the selection of individuals during the formation of a school is provided by certain mechanisms (Krause et al., 1996a, 1996b; Peuhkuri et al., 1997). First of all, the homogeneity of the size composition is achieved due to the passive exit from the school of smaller individuals, which, not possessing sufficient locomotor abilities, sooner or later lag behind the school. A decrease in the probability of association of fish of different sizes as part of a single school can be caused by a mismatch of biotopic preferences in fish of different sizes, for example, different attitudes to depth, illumination, flow, or the presence of shelters. It has also been established that the reaction of attraction to conspecific individuals, inherent in schooling fish, is best manifested in relation to individuals of similar size (Keenleyside, 1955; Ranta et al., 1992a; Krause, 1994; Krause and Godin, 1994). The unification of the size composition also occurs due to the fact that predators, as demonstrated by various examples, disproportionately eat those individuals out of heterogeneous schools that stand out for their size (Theodorakis, 1989). The size homogeneity of fish schools increases after predator attacks (Pitcher et al., 1986; Ranta et al., 1992b), which can be achieved not only due to the extermination of individuals marginal in size, but also due to the breakup of the school into two more homogeneous in composition or more independent schools or redistribution of individuals between neighboring schools.

In heterogeneous schools, small individuals find themselves in much less favorable conditions for feeding. It was found experimentally (Krause, 1994) that the competitive ability of large individuals is much higher: in a school of the common chub *Squalius cephalus*, which consists of two size groups equal in number (the ratio of average body lengths is 0.66 : 1.00), the share of larger individuals accounted for >85% all food consumed. A decrease in the proportion of large individuals led to an increase in food consumption by smaller fish. It is assumed that the avoidance by small fish of shoaling together with large fish will minimize food competition between partners. On the other hand, the feeding activity of single large individuals in a school of smaller fish is also suppressed (Peuhkuri, 1997, 1998). These features serve as the main mechanisms leading to the unification of the size of fish in a school.

Data on the size composition of juvenile fish schools are more contradictory. Using the Eurasian minnow as an example, it was found that juveniles do not unite in a single school if the difference in body length exceeds a certain value (Berwein, 1941). At the same time, according to multiple observations made by Radakov (1973), juveniles of the big-scale sand smelt, which differ taggedly in size, easily form a joint school. A higher level of size heterogeneity in the composition of schools of larvae and juveniles than in adult fish is shown in a large number of specific examples and, apparently, can be considered either as one of the features of schooling behavior of juvenile fish, or an insufficient development in it of those mechanisms that lead to homogeneity of schools of adults.

Species Composition of Fish in Schools

Migrating schools of fish, especially small pelagic species with high numbers, are characterized in most cases by exceptional homogeneity of the species composition. For marine pelagic planktonophagous fish, there is limited evidence indicating the presence of any species-specific outsiders in their schools (Hobson, 1963; Parrish, 1989). A short-term association of representatives of different species of marine pelagic fish into one school or aggregation can probably occur only during fattening in places of concentration of forage organisms, where schools of different fish are dispersed for feeding. In larger marine fish, especially pelagic predators, multispecies schools appear to form

more frequently. For example, mixed schools are common for the Atlantic mackerel *S. scombrus* (Pitcher and Parrish, 1993), the yellowfin tuna *T. albacares*, and the skipjack tuna *Katsuwonus pelamis* (Matsumoto et al., 1984; Hallier, 1991).

A different situation can be observed in coastal schooling tropical fish, similar in lifestyle and diet, as well as in size, shape, and body color, inhabiting the same biotopes. Large multispecies schools, uniting predominantly herbivorous representatives of different genera and families, can often be found among coral reefs (Ogden and Buckman, 1973; Itzkowitz, 1977). Parrot fish (Scaridae) living in the coastal areas of tropical seas—the blue tang *Acanthurus coeruleus* and the midnight parrotfish *Scarus coelestinus* form joint schools, the number of which reaches 50−400 individuals. However, the share of the midnight parrotfish in such schools is relatively small and does not exceed a few percent (Alevizon, 1976). In schools of *A. bahianus*, numbering many hundreds of individuals, representatives of other species of this genus are usually found—the blue tang surgeonfish and the doctorfish *A. chirurgus*. The absence of heterospecific individuals in schools of *A. bahianus* is an exception (Mochek, 1987). In turn, many fish species are also present in schools of the blue tang surgeonfish—surgeonfishes *A. bahianus* and *A. chirurgus*, the Bermuda chub *Kyphosus sectatrix*, various parrotfishes *Scarus* spp., the West Atlantic trumpetfish *Aulostomus maculatus* and even goatfishes such as the yellow goatfish *Mulloidichthys martinicus* and the spotted goatfish *Pseudupeneus maculatus* (Morgan and Kramer, 2004). It is interesting that such tolerance to the presence in a school of fish of other species, often unrelated ones, is combined in the blue tang with changes in the behavior model from schooling to territorial or transition to solitary movements, for example, to places of sanitary treatment by the cleaner-fish (Morgan and Kramer, 2004, 2005).

Joint schools are formed by the parrotfishes—*S. croicensis*, *S. radians*, *Sparisoma viride*; grunts (Haemulidae)—bluestriped grunt *Haemulon sciurus*, yellow grunt *H. flavolineatum* and common grunt *H. plumierii ronki*; sea perches (Lutjanidae)—schoolmaster snapper *L. apodus*, grey snapper *L. griseus*, dog snapper *L. jocu*; wrasses (Labridae)—blackear wrasse *Halichoeres poeyi*, slippery dick *H. bivittatus*, bluehead wrasse *Thalassoma bifasciatum* (Mochek, 1987). Joint schools are formed by juvenile parrotfishes *Chlorurus sordidus*, *C. bleekeri*, *C. gibbus*, *S. spinus*, and *S. schlegeli* (Crook, 1997), which have a similar body color, or adults of the whitetail dascyllus *Dascyllus aruanus* and reticulated (two-striped) dascyllus *D. reticulatus dascilli* (Losey, 2003). Among several dozen schools of surgeonfish *A. bahianus* caught in the coastal area, single specimens of the parrotfish *S. taeniopterus* are often found. Completely monospecies schools were an exception (Debrot and Myrberg, 1988). The chromis *Chromis nitida* and *C. atripectora-*

lis stay near coral reefs either in nearby but clearly separated schools or form joint schools (Sackley and Kaufman, 1996). The entry of individuals of outsider species into schools can occur with different ease in different biotopes. Underwater tracking of the striped red mullet *M. surmuletus* while feeding in shallow coastal waters revealed that small schools of these fish found on a flat and open sandy bottom were mainly monospecies, while when they were found among stones and thickets of aquatic vegetation, they often included wrasses and seabreams (Sparidae)—Mediterranean rainbow wrasse *Coris julis*, East Atlantic peacock wrasse *S. tinca*, common two-banded sea bream *Diplodus vulgaris*, sargo *D. sargus* and some others (Ajemian et al., 2016). In his monograph, Mochek (1987) gives a large number of examples of the composition of multispecies fish schools in the coral reefs of the southern shelf of Cuba. Some of the coral reef fish (grunts) form common schools with crustaceans of the genus *Mysidium*, which are similar to these fish in size, body shape, and behavior (McFarlad and Kotchian, 1982).

Usually, individuals of one species dominate in numbers in multispecies schools, while fish of other species make up a clear minority (Soin et al., 1981; Morgan and Kramer, 2004; Ajemian et al., 2016). In fish of different species, the tendency to form mixed schools is different. Thus, an analysis of the species composition of a large number of freshwater fish schools (Holubová et al., 2020) found that the common bleak *Alburnus alburnus* always forms monospecies schools; the bream *Abramis brama* in most cases forms monospecies schools, although some fish of other species may be found in some bream schools; for the common roach *Rutilus rutilus* and the perch *Perca fluviatilis*, mixed schools are more typical (Fig. 7).

Location in a school, swimming speed, distances between fish of different species in mixed schools differ, and the more, the less similar fish are to each other phenotypically and in other features. Thus, the yellow-eyed mullet and the large Australian salmon *Arripis trutta*, which have an elongated body, are distributed more homogeneously in joint schools, while the relatively high-bodied Australasian snapper *Pagrus auratus* in such schools kept separate and in less cohesive shoals (Middlemiss et al., 2019).

The formation of multispecies schools is most often observed in juvenile fish, especially in the first year of their life (Disler, 1960; Dmitrieva, 1967; Girsa, 1973; Ribbink et al., 1980; Peuhkuri et al., 1997; Krause et al., 1998). For example, juveniles of the Cherskii's thicklip gudgeon *Sarcocheilichthys szerskii* live in schools of the Amur minnow *Rhynchocypris lagowskii* and the stone moroko *Pseudorasbora parva* (Nikol'skii, 1974). Mixed schools are formed by larvae and early juveniles of the lavaret *Coregonus lavaretus* and the vendace *C. albula* (Lapin et al., 1978); in schools of the Eurasian minnow juveniles, larvae of
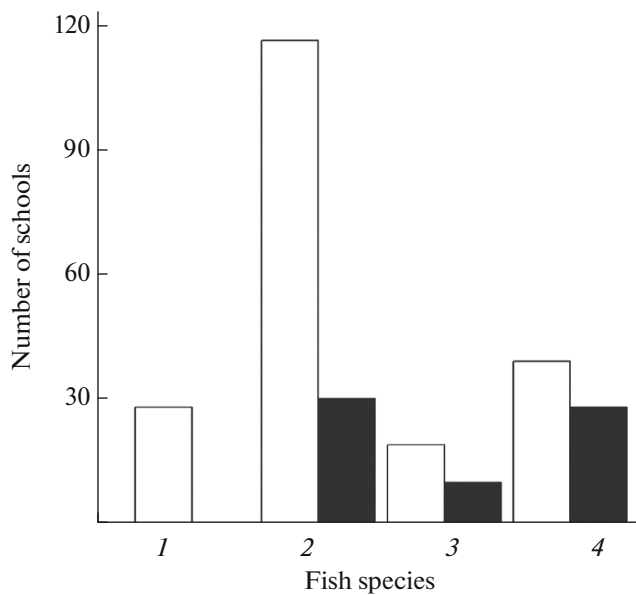
Fig. 7. Number of monospecies schools (□) and schools with the presence of individuals of other species (■) in the common bleak *Alburnus alburnus* (*1*), the bream *Abramis brama* (*2*), the European perch *Perca fluviatilis* (*3*) and the common roach *Rutilus rutilus* (*4*), observed at underwater video recording in a natural reservoir (according to: Holubová et al., 2020).

the commom dace *Leuciscus leuciscus* and the common roach can be found (Soin et al., 1981). Joint schools of juveniles of the golden shiner and the banded killifish also include juveniles of the white sucker *Catostomus commersonii*, the three-spined and the four-spined stickleback *Apeltes quadracus*. Approximately two thirds of the 34 studied schools of the golden shiner were heterogeneous in species composition; in more than 90% of cases, multispecies schools included juveniles of one or two additional species (Krause et al., 1996a). In schools of juvenile fish that are heterogeneous in species composition, one dominant species is often singled out, the representatives of which form the basis of mixed schools. For example, in schools of the juvenile minnows, this species accounts for up to 95−99% of the total number of individuals (Soin et al., 1981), and in schools of the golden shinner juveniles, ~71% (Krause et al., 1996a). Sometimes representatives of different species can make up equal or similar proportions in a school (Tanasiychuk, 1947).

Uniting of fish of different species into a single school gives them certain advantages, primarily in connection with feeding, since even a slight difference in preferred forage objects leads to a noticeable decrease in food competition in a school and to a more complete use of the food resources of the biotope (Ehrlich and Ehrlich, 1973; Wolf, 1985, 1987). Herbivorous coral fish in large mixed schools more easily overcome the resistance of territorial fish and eat

plants located in individual areas protected by other fish (Barlow, 1974; Vine, 1974; Alevizon, 1976; Robertson et al., 1976; Hara, 1985a, 1985b; Marsh and Ribbink, 1986). Uniting of fish of different species commonly leads to formation of larger schools, which is beneficial to all individuals due to advantages that arise in feeding, as well as in protection from danger (Ehrlich and Ehrlich, 1973; Sackley and Kaufman, 1996).

At the same time, mixed schools are less cohesive, and the behavior of fish of different species differs (Paijmans et al., 2022). Therefore, "outsider" fish present in schools, especially if there are few of them, are clearly visible and are primarily exterminated by predators. Undoubtedly, the increased vulnerability of such fish is one of the reasons for the short existence of mixed multispecies schools. The risk of being caught during a predator attack is especially high if an individual of a different species, which differs from other members of a school, is in a small school. The larger the school, the relatively more protected in them are fish of other species or other sizes that have some individual differences from other individuals in color or behavior (Landeau and Terborgh, 1986). The divergence of fish of different species and the formation of several monospecies schools from one mixed one also occurs under the direct threat of a predator attack (Wolf, 1985). Often, when an immediate danger arises, mixed schools break up into several smaller schools that are more homogeneous in terms of species. This feature was discovered when observing the behavior of a school artificially composed of several species of cyprinids—the Eurasian minnow, the dace and the gudgeon *Gobio gobio*. In the presence of a predator (a model of the pike *Esox lucius*), the probability that a conspecific individual turned out to be a school partner significantly increased (Allan and Pitcher, 1986).

Interestingly, even when joint schools are formed, individuals of different species in a school are usually close in size. This was discovered in the course of a special study (Krause et al., 1996a), which compared the body sizes of the juvenile golden shiner and the banded killifish in joint schools. Juveniles of these species often form such schools in coastal shallow waters of lakes in North America. Only those schools that were completely caught and in which the number of individuals of both species was sufficient for statistical comparisons were analyzed. It turned out that schools caught in the same place of the lake can differ by almost two times in the average size of the fish included in them (total for both species). However, the sizes of individuals of different species within the same school differ less—the difference was statistically significant only in 7 out of 12 joint schools, and in some of them, individuals of the golden shiner were larger, in others, of the killifish (Fig. 8). Thus, the mechanisms that ensure the dimensional assortative compo-
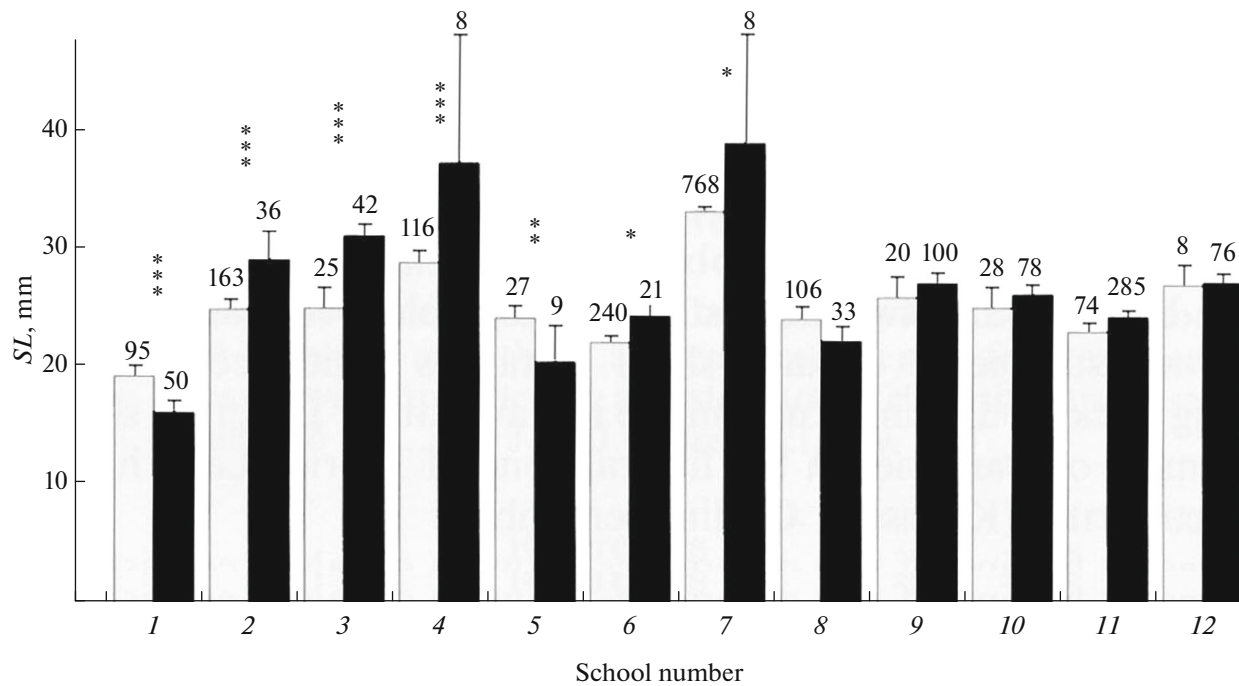
Fig. 8. Average standard length (*SL*) of juveniles of the golden shiner *Notemigonus crysoleucas* () and the banded killifish *Fundulus diaphanus* (■) in 12 different joint schools. The number of individuals of each species in the school is given by numbers above the columns; (□)—95% confidence interval; differences in body length between fish of two species in a school are significant at *p*: * < 0.05, ** < 0.01, *** < 0.001 (according to: Krause et al., 1996b).

sition of multispecies schools are equally effective for fish of different species.

VARIABILITY OF THE COMPOSITION OF SCHOOLS

Fish schools are temporary associations, their composition remains constant for a very short time, which usually does not exceed daylight hours. As was established using genetic methods, even schools of the juvenile three-spined stickleback, still under the protection of a male, unite individuals that originally belonged to different family groups and are not descendants of the same pair of spawners (Peuhkuri and Seppä, 1998). In this respect, fish differ from many other vertebrates, in which family groups (broods, prides) and large social groupings (schools, flocks, herds) persist for a longer time, and their composition, as a rule, is characterized by high stability (Manning, 1979).

Fish schools have the ability to easily split up into smaller schools or combine into larger ones. The association of schools can occur when two or more schools meet by chance, for example, when searching for food or at places of fattening and resting of fish, when making migrations. Relatively large fish schools also easily break up into smaller ones—when frightened, when a school performs complex and fast maneuvers. Pictures of the association and disintegration of schools are

especially clearly visible when observing the behavior and movement of schools of juvenile fish in natural conditions. The rapid process of combining individual schools or appearing smaller independent schools from one common school is characteristic of migratory adult fish and is often recorded, for example, when observing the movements of commercial fish from an airplane (Tokarev, 1953).

The time during which the composition of the school is relatively stable and does not change significantly may be limited to only a few minutes or hours. Thus, according to the observations of Radakov (1973), the European anchovy in a large basin keeps in small, actively moving schools with clear boundaries. However, the duration of the existence of individual schools is only a few tens of seconds or even less − the high mobility of the fish leads to the fact that, colliding with each other, the schools join into one, which can again be divided into two or more. This behavior of fish makes it difficult to calculate the total number of schools in the pool.

The collision of schools, their association and subsequent divergence into two or more new ones leads to a rapid redistribution of individuals. In the experiment, all specimens of the Black Sea picarel *Spicara smaris*, which are provided with color marks, initially stay in one school together with untagged fish, but the very next day they can be found in different schools (Radakov, 1973). During the first day, tagged individ-

uals of the banded killifish released into the wild were distributed among different schools (Hoare et al., 2000b). Observations of tagged individuals of the skipjack tuna in the open ocean have shown that fish easily move from school to school and do not show a noticeable tendency to stay in any of them for a long time (Hilborn, 1991). The mass release of tagged skipjack individuals and their repeated catch, carried out for a long time, fully confirmed this conclusion—after 1 month, many tagged individuals met in different schools, and after 3–5 months, this was observed in almost all cases (Bayliff, 1988). However, according to data obtained for the yellowfin tuna, tagged fish could remain loyal to the same school and place for more than six months (Klimley and Holloway, 1999).

Data characterizing the frequency of random collisions between different schools are extremely scarce, despite the long history of studying the schooling behavior of fish and a large number of studies and observations. It is believed that random encounters of moving schools occur more often in freshwater fish than in marine pelagic fish (Croft et al., 2003b). According to available data, in freshwater fish, golden shiners and guppies, such encounters are recorded on average every 1.1 min and 14 s, respectively (Krause et al., 2000; Croft et al., 2003a), while in the Atlantic herring, they occur every 13.7 min (Pitcher et al., 1996), more often at night than during daylight hours (Mackinson et al., 1999). On average, meetings of schools are short-term; in small lake fish, such as the three-spined stickleback, the golden shiner, the banded killifish, and others, they last 3.7 s (Krause et al., 2000). The patterns of fish behavior during collisions between different schools and the specific reasons that encourage fish to joint are still far from being understood. These important issues affect many basic mechanisms, such as the formation and dynamics of school composition, the exchange of information between schools, the spread of infections, and others (Croft et al., 2003b).

However, there is evidence that the composition of schools is not formed randomly (assortativity) and, therefore, may be more stable over time. Thus, it has been experimentally shown that fish, for example, the three-spined stickleback and others, prefer to joint in a school with familiar conspecifics and, to a lesser extent, with individuals which they have not met before (Brown and Colgan, 1986; Van Havre and Fitz-Gerald, 1988; Farmer et al., 2004; Ward et al., 2020). However, these interesting facts require verification and so far, cannot be considered as serious arguments in favor of the hypothesis of the stability of the school composition.

Only when living in places isolated from each other or in fish with a weak ability to move is a relatively high stability of the composition of schools possible. This is typical, for example, for juveniles of the yellowtail *Seriola quinqueradiata*, which at an early age stay among small tufts of seaweed *Sargassum* sp. floating on the surface of the water. Settling immediately after metamorphosis in an isolated accumulation of algae, the yellowtail juveniles do not leave it until this temporary shelter is destroyed (about a month). The juveniles migrate to a new closest floating aggregation of algae simultaneously with the whole school, thus keeping their composition unchanged (Safran, 1990; Safran and Omori, 1990; Sakakura and Tsukamoto, 1997). Signs of relative stability of the school composition were found in the three-spined stickleback. Small schools of these fish were caught near the shore in a flow channel, all individuals of the school received individual marks, and they were released again at the place of capture. Repeated catches found that individuals that were originally part of the same school could be in the same school even five days after marking. However, the number of such individuals, as well as the total number of tagged fish recaptured, declined rapidly over five consecutive days (Ward et al., 2002).

Many schooling fish, while not territorial or migratory, adhere to certain stable areas and move within them. Individual marking of the schooling parrotfish *S. rivulatus* and long-term tracking of tagged individuals showed that the schooling movements of these fish *TL* ~24 cm are limited to a relatively small section of the coral reef, ~250 m in length (Welsh and Bellwood, 2012).

The main reason for the instability of the composition of schools is their daily cycle of breakup and formation. With the onset of evening twilight, fish schools gradually lose their clear outlines, the distance between individuals increases, and as a result, at night, either loose, amorphous groupings are formed that unite fish of several different schools, or the fish disperse over a larger area, for example, due to the current (Manteifel' et al., 1965; Girsa, 1973). In the morning, with an increase in illumination, fish schools form again. There is no information indicating that these schools combine former partners in themselves. Moreover, there are direct indications that this does not occur in real conditions, and individuals that were previously part of one school can be found in other schools after a short time.

CONCLUSIONS

Thus, fish schools are characterized by a high level of size and species uniformity, which is provided by various mechanisms—the intention to unite with conspecifics of close length, the elimination of physically less sturdy individuals from a school; selective extermination of individuals that differ in their size, color, behavior and other external features. Homogeneity is most pronounced in migrating schools and in schools of pelagic fish. The higher the proportion of "outsider" individuals in a school, the shorter the duration of the existence of such schools. Even fish schools that are homogeneous in composition are extremely unsta-

ble and within a short time can repeatedly break up and re-form, but in a different composition. This property is a characteristic feature of fish schools and distinguishes them from social groupings of various types of other vertebrates.

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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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