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Internal Structure of a Fish School

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Abstract—Regularities of arrangement of fish in schools have been considered. In migrating isotropic schools, the internal structure is most ordered, the fish in them are oriented strictly parallel to each other, the partners are located at an equal distance and with a characteristic (rhomboid) displacement relative to each other in the horizontal plane. The location of fish in such schools is influenced by the physical forces of hydrodynamic vortices created by swimming fish (hydrodynamic wake). In isotropic schools, fish maintain a certain distance between themselves (linear distance) and a certain displacement (frontal, vertical and horizontal) relative to each other. The average density of schools varies greatly and depends on the size of fish, the swimming velocity or the flow of water to overcome, the level of illumination and other factors. In large schools, the average density of fish is higher in the center and decreases towards the periphery of a school. Fish in schools form intra-school subgroups of three to five individuals, within which fish are placed strictly in a horizontal plane, or with a slight vertical displacement. The mutual arrangement of fish in a subgroup is constantly changing, and the distance between partners is less than the distance to any individual of another subgroup. Existing data on individual spatial preferences of fish in schools has been analyzed.

Keywords: fish, schooling behavior, fish school structure, isotropic schools, intra-school groups, school density, spatial preferences of fish in schools

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The spatial arrangement of fish in a school, or the internal structure of schools, has been studied mainly on the example of migrating flat schools. In such schools, fish are oriented strictly parallel to each other, partners are located at an equal distance from each other in a horizontal plane. For example, in the saithe *Pollachius virens*, the average angle of inclination of the longitudinal axis of the fish body to the horizontal plane is only 0.9° ± 5.4° (Foote and Ona, 1987). The mutual arrangement and distance between partners in a school is not accidental, but obeys certain rules.

When observing schools of swimming fish in nature or in aquariums and pools, one can easily see that fish in migrating schools are displaced relative to each other in a horizontal plane, arranged in a checkerboard or rhomboid pattern (Fig. 1). Such schools are called *isotropic schools.* The location of fish in an isotropic school is determined, among other things, by the physical forces that arise in the aquatic environment when fish swim. Theoretical calculations performed back in the 1930s by the well-known hydrophysicist, academician V.V. Shuleikin, showed that between two closely spaced bodies moving in the same direction, the so-called *ponderomotive forces* act, the magnitude of which is determined by the mutual arrangement of these bodies (Fig. 2) (Shuleikin, 1968). If the angle between the direction of movement of the bodies and the segment connecting their centers, the so-called *course angle*, is more or less than 54°40′, then the action of forces bringing the bodies together exceeds or is inferior to the action of repulsive forces. The angle of direction to neighboring partners, calculated on the basis of acting ponderomotive forces, corresponds to the size of this angle in actually observed schools of fish (Cullen et al., 1965; Serebrov, 1984). The magnitude of ponderomotive forces is proportional to the fourth power of the body length of fish; therefore, in schools of small-sized individuals, such forces are relatively small and do not have such a significant effect on the behavior of fish as in schools of larger individuals. This explains the fact that in schools consisting of small fish, the arrangement of individuals relative to each other is not so noticeably subject to a checkerboard pattern, while in schools of large fish, for example, in tunas (Thunnini), swimming at high speed, this order is maintained much stricter.

The checkerboard pattern of fish swimming in a school is due not only to the action of ponderomotive forces arising at this time, but also to other features of the hydrodynamics of swimming and the energetics of swimming fish. Actively moving or being in the current, the fish create hydrodynamic disturbances in the water—a gradually weakening peculiar turbulent *hydrodynamic wake* (Fig. 3). This wake is symmetrical

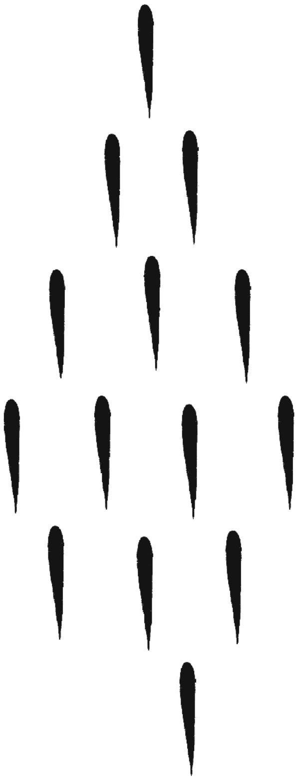

Fig. 1. Arrangement of fish in isotropic migrating schools.

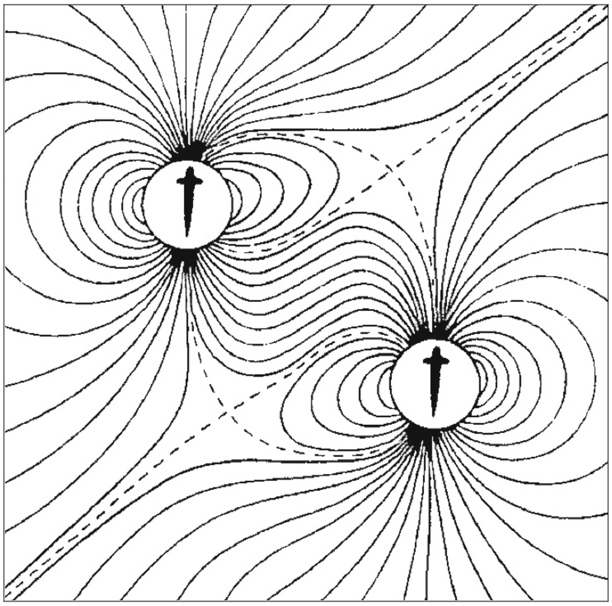

Fig. 2. Scheme of hydrodynamic forces of repulsion and convergence, at which their mutual balancing occurs during schooling swimming of fish (according to: Shuleikin, 1968).

with respect to the longitudinal axis of the fish body and represents a *system of decaying microvortices* (microeddies), which break off the edge of the caudal fin when water flows around the surface of the fish body. Microvortices are created both during the active movement of fish due to the work of the main movers—the caudal fin and the caudal peduncle, and in fish standing in the current. In the turbulent environment that is created in a school, the fish avoid following the individual in front, and are located away from it. The conditionality of the location of fish in a school by physical laws served as the basis for formulating *hydrodynamic hypothesis of fish school formation* (Belyayev and Zuyev, 1969). According to this hypothesis, the energy expended by fish for swimming is less if they are in a school, and higher in solitary individuals.

Fish not only arrange themselves in a certain way relative to each other, creating the spatial structure of the school, but also tend to maintain a well-defined distance between themselves, which is approximately the same between neighboring pairs (Hunter, 1966; Inagaki et al., 1976; Aoki, 1980; Partridge, 1981). The distance to a neighboring school partner can be characterized by several different values or indicators: R_l—linear distance, i.e., the length of the line connecting two neighboring fish; S_f—frontal displacement, or the distance between parallel swimming paths of two neighboring fish; S_v—vertical displacement, or the distance in the vertical plane between the swimming horizons of two neighboring fish; S_h—horizontal displacement, or displacement of individuals relative to each other in the horizontal plane (Fig. 4). The linear distance between individuals in migrating schools usually ranges from 2–3 to 4–5 average body lengths of fish (L) (Table 1), sometimes it can be much less (Breder, 1965, 1967; Zuyev and Belyayev, 1970; Serebrov, 1984). With the help of underwater stereophoto equipment, it was found that in natural conditions the linear distance between individuals in schools of the Japanese jack mackerel *Trachurus japonicus* (body length ~ 20 cm) and the mackerel *Scomber* sp. (~16 cm) is 1.43 and 1.51L, respectively (Aoki et al., 1986). In schools of the Atlantic herring *Clupea harengus*, the distance to the nearest partner averages 0.82L, and when frightened, it can be even less, 0.77L (Pitcher and Partridge, 1979; Partridge et al., 1980; Domenici et al., 2000). Under artificial conditions, the relative distance between partners can be even less: when keeping the herring *Harengula* sp. in a pool, the distance between the nearest schooling partners was only 4.4 cm, while the body length of the fish was ~7.5 cm (Cullen et al., 1965); i.e., ~0.6 body length. For a more accurate idea of the real distance between fish in schools, it is proposed to estimate the distance to several closest partners and determine the ratio between these values. The closer it is to 1 : 1, the more ordered (homogeneous) the school structure is (Partridge et al., 1980).

The value of the linear distance varies in accordance with the normal distribution (Fig. 5), which emphasizes the intention of fish in a school to maintain the optimal distance between themselves (Sere-

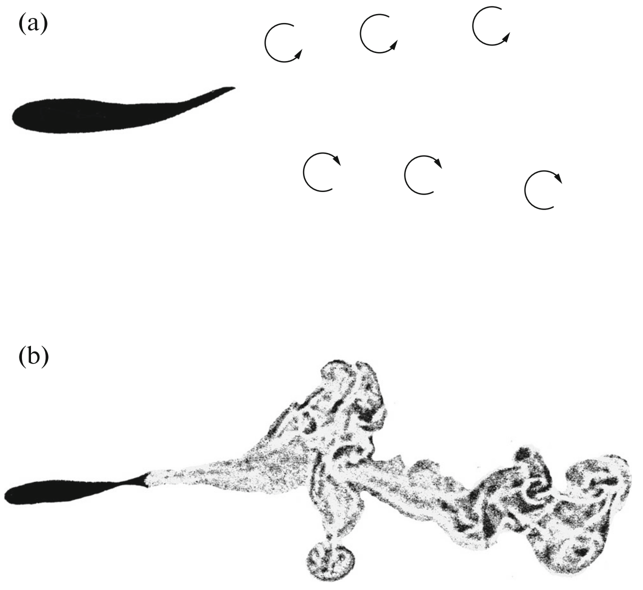

Fig. 3. Schematic diagram of hydrodynamic vortices created by swimming fish (a) and hydrodynamic disturbances left by swimming fish (b) in a shallow aquarium with a sharp vertical temperature gradient (2°C/cm). Visualization of disturbances was created due to different refraction of light rays (according to: McCutchen, 1976).

brov, 1984). The calculations performed show that coefficient K, calculated as the ratio of the linear distance to the average body length, for fish from migrating schools can be expressed in close values: $K = R_l/L \approx 2.44$ (K values vary from 2.19 to 2.75), as was shown for a number of marine pelagic fish species (Serebrov, 1976). However, according to other researchers, this value may be different. In schools of the Black Sea horse mackerel *T. mediterraneus ponticus* with a body length of 16–20 cm, when observing their behavior in a flowing-water pool (flow velocity 1.2 m/s), the distance between individuals does not exceed 2–3 body thicknesses (most often 0.5–1.0 body thicknesses) (Zuyev and Belyayev, 1970). The frontal displacement of fish in schools is slightly less than the linear distance, and the vertical displacement is much less than the linear distance and frontal displacement. In migrating schools of the capelin *Mallotus villosus*, as follows from the analysis of photographs taken directly in schools of these fish, the course angle between neighboring individuals located at a distance of about three body lengths (46 cm) from each other is equal to 32° in the vertical plane, then as in the horizontal plane its value is greater—54°40′ (Serebrov, 1984). In schools of the Black Sea horse mackerel, the vertical displacement is about 0.5 of the body thickness of the

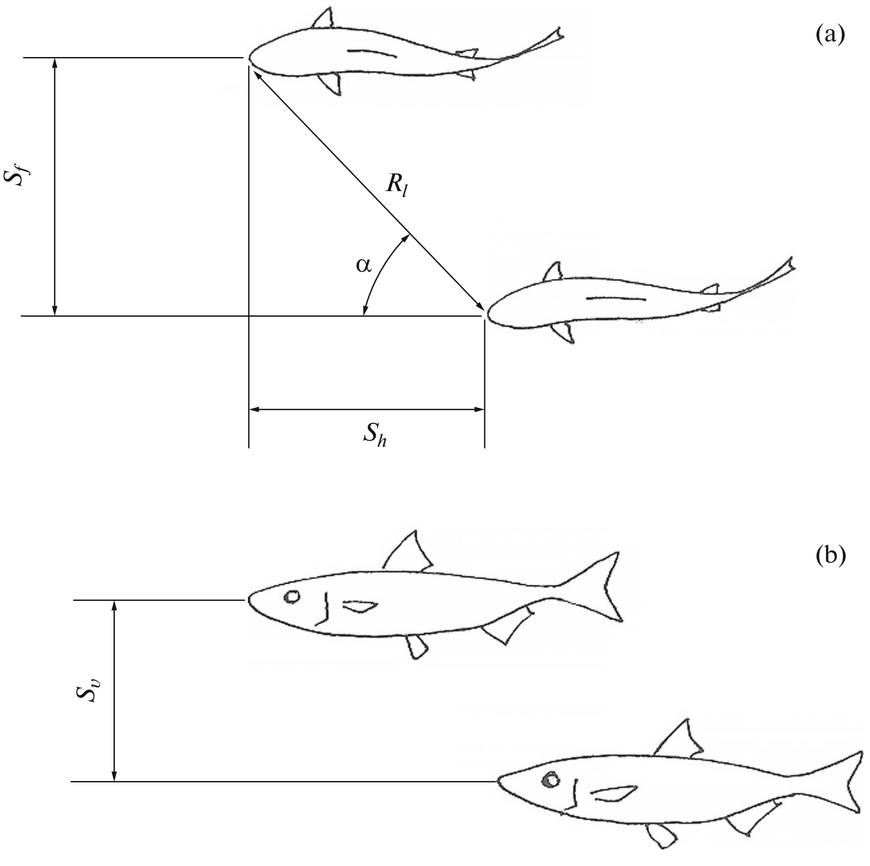

Fig. 4. Values characterizing the relative position of neighboring fish in a school: R_l—linear distance; S_f, S_h, S_v—frontal, horizontal and vertical displacement, respectively; α—course angle. View: a—top, b—side.

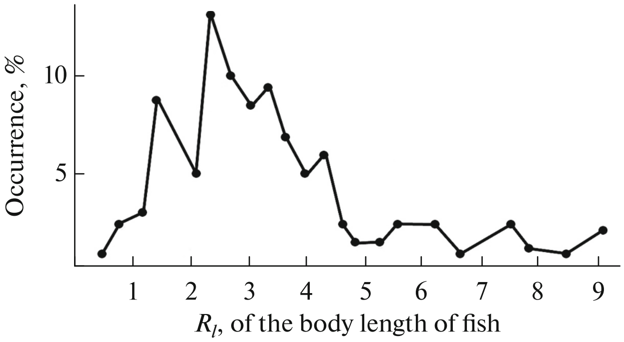

Fig. 5. Distribution of linear distance values (R_l) between closest partners in schools of capelin *Mallotus villosus* with an average length of 15.22 cm (according to: Serebrov, 1984, modified).

fish, and the horizontal displacement usually varies within 0.25–0.75*L* (Zuyev and Belyayev, 1970). The location of fish in a school relative to each other in the horizontal and vertical planes is shown in Fig. 6.

In certain situations, the position of the individuals in a school may be less stable or depend on some factors. A decrease in illumination leads to an increase in the distance between the nearest partners in a school (Azuma and Iwata, 1994). In artificially mixed schools of cyprinids (Cyprinidae), the larger dace *Leuciscus leuciscus* (14 cm) is always at the head of the school, while the Eurasian minnow *Phoxinus phoxinus* (5–6 cm) and the gudgeon *Gobio gobio* (9 cm) are always, i.e., at any combination of the composition of the school, located in its rear part, occupying more upper (minnow) or lower (gudgeon) horizons. Observations of fish with individual color marks showed that the position of individuals of all three fish species in mixed schools is less stable compared to the behavior of the same fish in monospecies schools (Allan, 1986). In multispecies schools of surgeonfish (Acanthuridae), representatives of the dominant blue tang surgeonfish, *Acanthurus coeruleus*, usually occupy the position at the head of a school, while small individuals of another species of surgeonfish, *A. bahianus*, stay in the rear part of the school (Morgan and Kramer, 2004).

SCHOOL DENSITY

The structure of an isotropic school, i.e., schools with a checkerboard arrangement of individuals corresponds to a geometric representation in the form of the densest "packing" in the space of spheres with a radius $R_l/2$, when the fish are located near the points of the tetrahedral lattice. This is confirmed by mathematical calculations and the actually observed arrangement of fish in schools (Zaferman, 1975; Serebrov, 1984; Zaferman and Serebrov, 1988). The spherical shape of the individual zone around the fish in the school is confirmed by strict three-dimensional measurements of their location (Middlemiss et al., 2018).

The ratio between the density of fish in a school, their average size and the distance between neighboring individuals is shown in Table 1, the relationship between the average length of fish and the distance between individuals in a school (linear distance) is shown in Fig. 7. There is a close correlation between the last two parameters (r = 0.979). The performed calculations show that the average absolute density of schools is inversely proportional to the third power of the linear distance between fish ($\rho = 1.4/R_l^3$) (Serebrov, 1976; Zaferman and Serebrov, 1988). A close agreement between the density of schools of the longspine snipefish *Macroramphosus scolopax* actually observed in nature and the calculated one is achieved only when using coefficient *K* for calculations for those fish species that are close to the longspine snipefish in body shape and some other morphological features, such as the ratio of the maximum deviation of

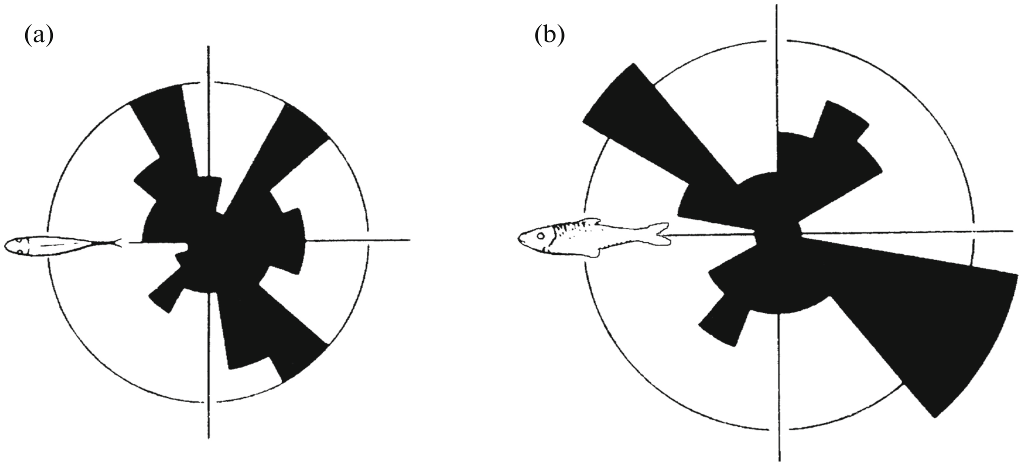

Fig. 6. Position of nearest individuals in fish schools in horizontal (a) and vertical (b) planes (according to: Cullen et al., 1965).

Table 1. Linear distance between neighboring individuals in migrating schools and the average density of fish schools (according to: Serebrov, 1976, with additions)

Fish species	Average length (L) of fish, cm	School density, ind./m^3	Linear distance (R_l), cm	Coefficient $K = R_l/L$
European anchovy *Engraulis encrasicolus*	11.8	33.00	31	2.62
Capelin *Mallotus villosus*	14.7	15.70	40	2.75
Polar cod *Boreogadus saida*	18.7	13.60	42	2.24
Atlantic cod *Gadus morhua*	27.9	4.70	61	2.19
Atlantic herring *Clupea harengus*	30.5	3.20	68	2.26
Roundnose grenadier *Coryphaenoides rupestris*	75.9	0.13	197	2.59
Sunbleak *Leucaspius delineatus*	4.6	578.70	12	2.60

the caudal fin from the longitudinal body axis during swimming to the body length of fish (Serebrov, 1976).

According to existing estimates, the average density of fish in migrating schools should be close to such a ratio that one individual has a volume of water equal to the cube of the body length of fish (L^3) (Pitcher and Partridge, 1979). However, real observations indicate that the density of schools varies significantly, while it can be much lower or higher than the indicated value, even according to data obtained for the same species. According to the estimates of some authors, in schools of Atlantic herring, on average, there are $0.7L^3$ per individual (Pitcher and Partridge, 1979), according to others—$1.15L^3$ (Domenici et al., 2000). In the latter case, estimates were made for a school of Atlantic herring surrounded by killer whales *Orcinus orca* hunting them and taking on a spherical shape characteristic of such a situation. The average density of fish in such schools was 24.6 ind./m^3, which is an order of magnitude higher than in schools of fish of the same size at the same time of the year and day, but not threatened by predators (Domenici et al., 2000). The average density, established from hydroacoustic estimates of 76 schools of Atlantic herring, was 4.25 ind./m^3 (with this indicator varying from 0.3 to 5.0 ind./m^3). This value is relatively stable and is repeated in estimates of the density of moving herring schools of various shapes in different years (Misund and Floen, 1993; Misund, 1993; Misund et al., 1995).

The average density of schools of the roundnose grenadier *Coryphaenoides rupestris* with a body length of ~ 65–80 cm is 1–2 ind./m^3 (Galaktionova and Galaktionov, 1990), and of Atlantic cod and haddock *Melanogrammus aeglefinus*, ~1 ind./m^3 (Konstantinov, 1977). This value varies widely. Thus, if the average density of schools of the Far Eastern sardine *Sardinops sagax* with a body length of ~15 cm is ~26 ind./m^3, then individual schools can differ in density by more than 100 times (Misund et al., 2003). With short intervals and in a wide range, the density of the same school changes, which can be easily judged, in particular, by the constantly changing area of the school (Fig. 8) (Misund et al., 1998). In the pre-spawning period, the density of fish in schools of the Pacific herring *C. pallasii* is much higher and amounts to several tens of fish per 1 m^3 (Gankov et al., 1953). In schools of the Japanese jack mackerel *T. japonicus*, the average number of fish with the length ~20 cm per 1 m^3 was 6.6; in schools of mackerel *Scomber* sp.—19.5 (Aoki et al., 1986), in schools of capelin, body length ~ 15–16 cm—1–3 ind./m^3 (Serebrov, 1984). The density of fish in a school, expressed as the volume per individual, correlates with the average distance to the nearest partner in the school. The relationship between these parameters in schools of the saithe *P. virens* is shown in Fig. 9 (Pitcher and Partridge, 1979).

With an increase in the speed of movement or when the fish enter the current, the compactness of the school noticeably increases (Pavlov, 1970; Pitcher and Partridge, 1979; Wiwchar et al., 2018). Thus, under natural conditions, the average distance between individuals in moving schools of Eurasian minnow juveniles (body length 17–32 mm) is 3.35 mm, while in immobile schools it is 4.80 mm (Serebrov, 1978). In

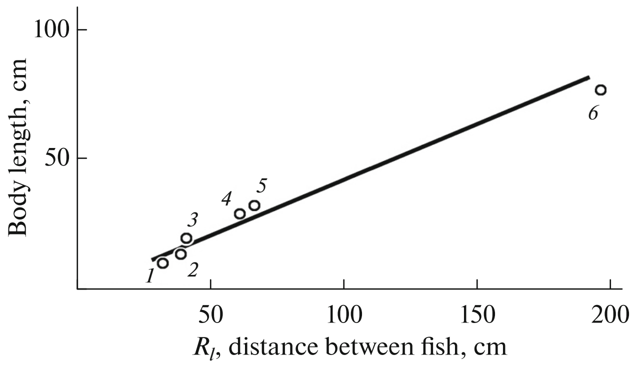

Fig. 7. Dependence of the distance between fish in a school (linear distance) on their average body length: *1*—European anchovy *Engraulis encrasicolus*, *2*—capelin *Mallotus villosus*, *3*—polar cod *Boreogadus saida*, *4*—Atlantic cod *Gadus morhua*; *5*—Atlantic herring *Clupea harengus*, *6*—roundnose grenadier *Coryphaenoides rupestris* (according to: Serebrov, 1976).

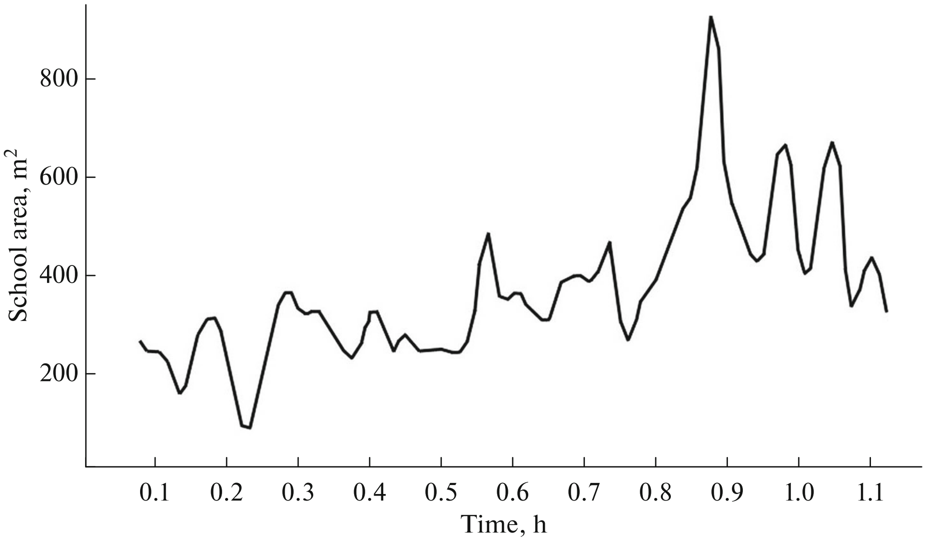

Fig. 8. Changes in the horizontal area of one of the schools of the Atlantic herring *Clupea harengus* off the coast of Northern Norway (according to: Misund et al., 1998).

proportion to the increase in the flow velocity, the mutual parallel orientation of individuals in the school increases, and the individuals in the school increasingly lose their rhomboid position relative to each other ("chessboard" formation) and increasingly occupy an equal position along the front of movement (Figs. 10, 11) (Inoue et al., 1979; Ashraf et al., 2017; Kent et al., 2019). It has also been noted that the average density within large schools is higher in the central areas and decreases towards their periphery. The central and edge parts of schools can differ in density by a factor of 10 or more (Fig. 12). In the center of large schools of Atlantic herring (body length of fish 34 cm), the density in some areas reaches 27 ind./m^3, the size of such areas ranges from several meters to several tens of meters (Misund, 1993; Misund and Floen, 1993).

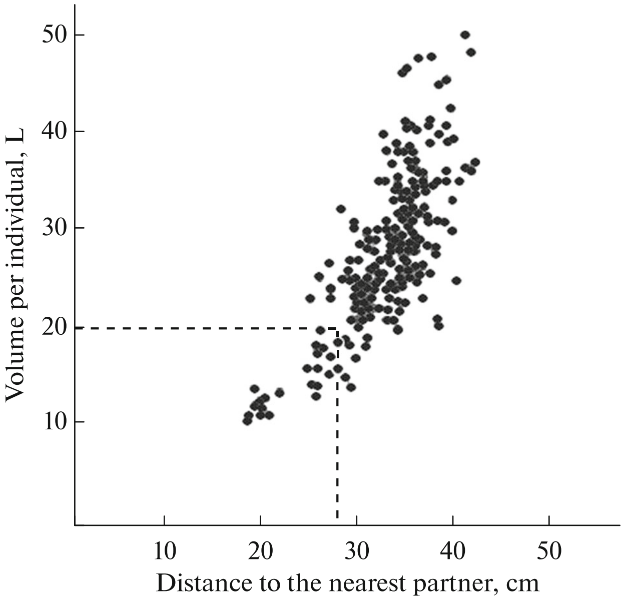

Fig. 9. Dependence of the volume per individual in schools of the saithe *Pollachius virens* on the average distance to the nearest partner in a school. The dashed lines indicate the values corresponding to the average length of the fish body (L) on the horizontal axis, to the cube of this length (L^3) on the vertical axis (according to: Pitcher and Partridge, 1979).

INTRA-SCHOOL GROUPINGS

Migrating schools of fish, despite their isotropy, are not absolutely homogeneous and ordered formations, but have a kind of "cellular" structure. The cellularity of a school is difficult to detect by visual methods of analysis, but it is detected by mathematical processing of the coordinates of the location of individuals in space (Serebrov, 1984; Zaferman and Serebrov, 1988). These cells are called *intra-school subgroups*. The number of fish in subgroups, as was found in the course of special studies of schools of capelin, Black Sea horse mackerel, haddock and other fish species, usually does not exceed 3–5 ind. (Aoki, 1980; Partridge, 1981; Serebrov, 1984; Zaferman and Serebrov, 1988). It is within these small subgroups that the highly ordered arrangement of fish relative to each other is realized. An analysis of fish swimming showed that even small schools of 20–30 individuals represent an association of subgroups. The mutual arrangement of fish in subgroups differs, but most often the fish line up either in a wedge or in a line, one slightly behind the other (ledge), and only much less often can one find a short swimming of two fish with their equal parallel relative position (linear front), when the horizontal displacement S_h is practically not expressed. The shape of the wedge can be symmetrical or asymmetri-

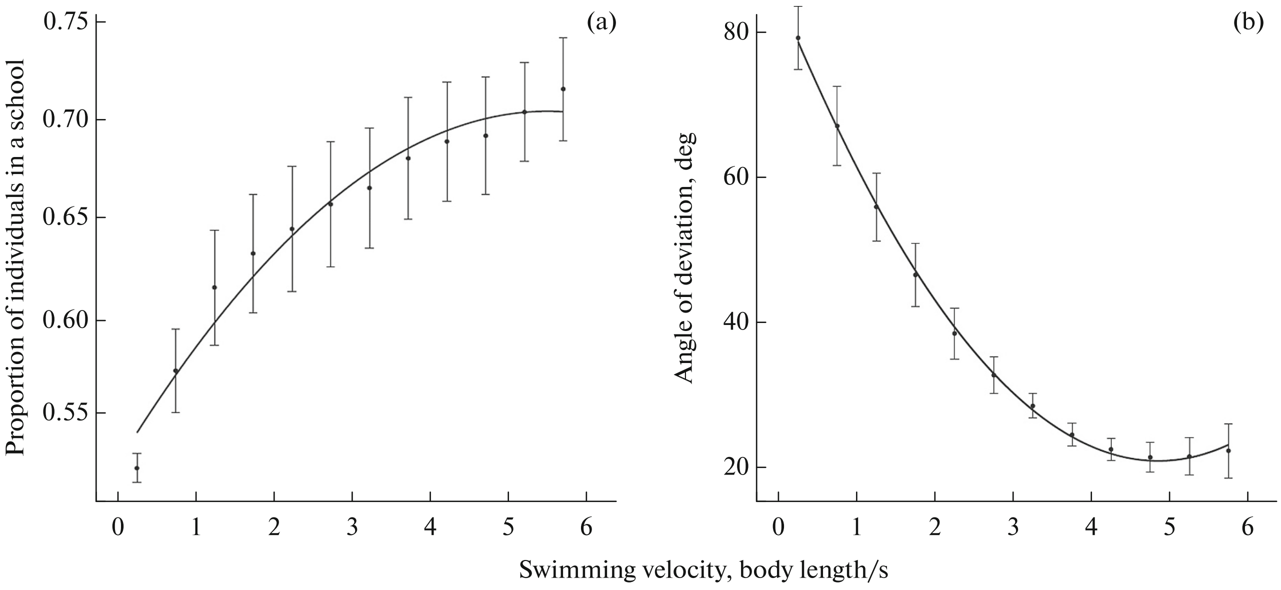

Fig. 10. Dependence of the proportion of fish in a school located at the same level with a focal individual (a) and the dependence of the average angle of deviation of the nearest partner in the school on the swimming velocity (b) in the silverside *Menidia* spp. (Melanotaenia) (according to: Kent et al., 2019): (●)—mean value, (I)—standard error, (——)—quadratic regression line.

cal (Fig. 13). The mutual arrangement of fish in intraschool subgroups is constantly changing, all fish are involved in the regrouping, regardless of whether they are in the front, in the middle, or in the back of the subgroup (Zuyev and Belyayev, 1970).

A special analysis of the location of individuals in schools, performed on the basis of photographs of capelin schools taken in nature, revealed that in these fish, subgroups most often (34.1%) consist of three individuals, somewhat less often, of 2, 4, or 5 ind. (20.5, 22.7 and 22.7% of cases, respectively) (Serebrov, 1984). The distance to a partner in subgroups is always less than the distance to any individual belonging to any other subgroup of the school. In subgroups, all fish are placed either strictly in one horizontal plane, or with a slight vertical displacement. It is assumed that such an arrangement can be caused not only by the hydrodynamic features of schooling swimming, but also by the creation of optimal conditions for controlling the movements of the nearest partners by lateral line receptors located on the lateral surface of the body (Zuyev and Belyayev, 1970).

The sizes of fish in subgroups practically coincide. Using stereo video recordings of schools of Atlantic herring and Atlantic mackerel *S. scombrus* to determine the distance between fish in more than 17000 pairs, it was found that fish tend to be located in a school next to similarly sized individuals. A high positive correlation in body length is observed between the closest neighboring fish in a school: 0.97 and 0.98 for herring and mackerel, respectively (Fig. 14). The preference to stay in a school next to individuals of similar size is maintained despite the fact that fish within the school are constantly moving: in herring (body length 21 cm), the change of the closest partner occurs on average 11 times per minute, i.e., every 6.2 body lengths passed by the fish, in mackerel (body length 31 cm)—6.2 times per minute or every 12.5 body

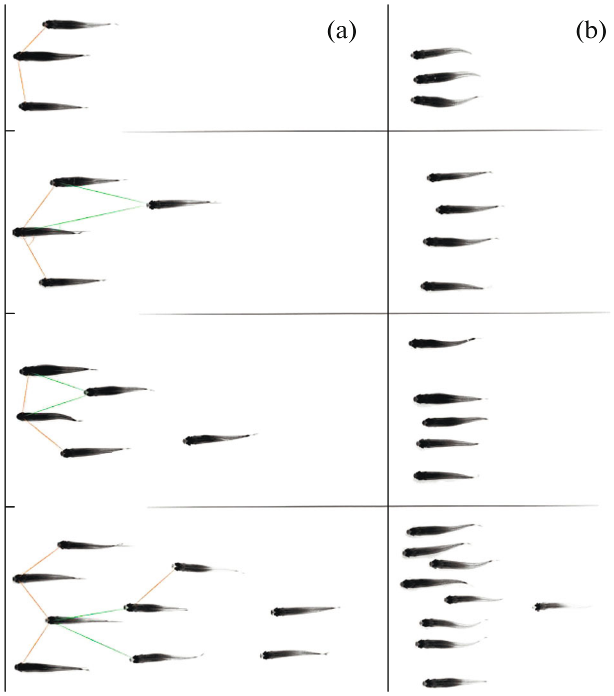

Fig. 11. Location of fish in the schools of tetra *Hemigrammus bleheri* of different numbers at the flow rate 0.77 *TL*/s (a) and 3.91 *TL*/s (b) (according to: Ashraf et al., 2017).

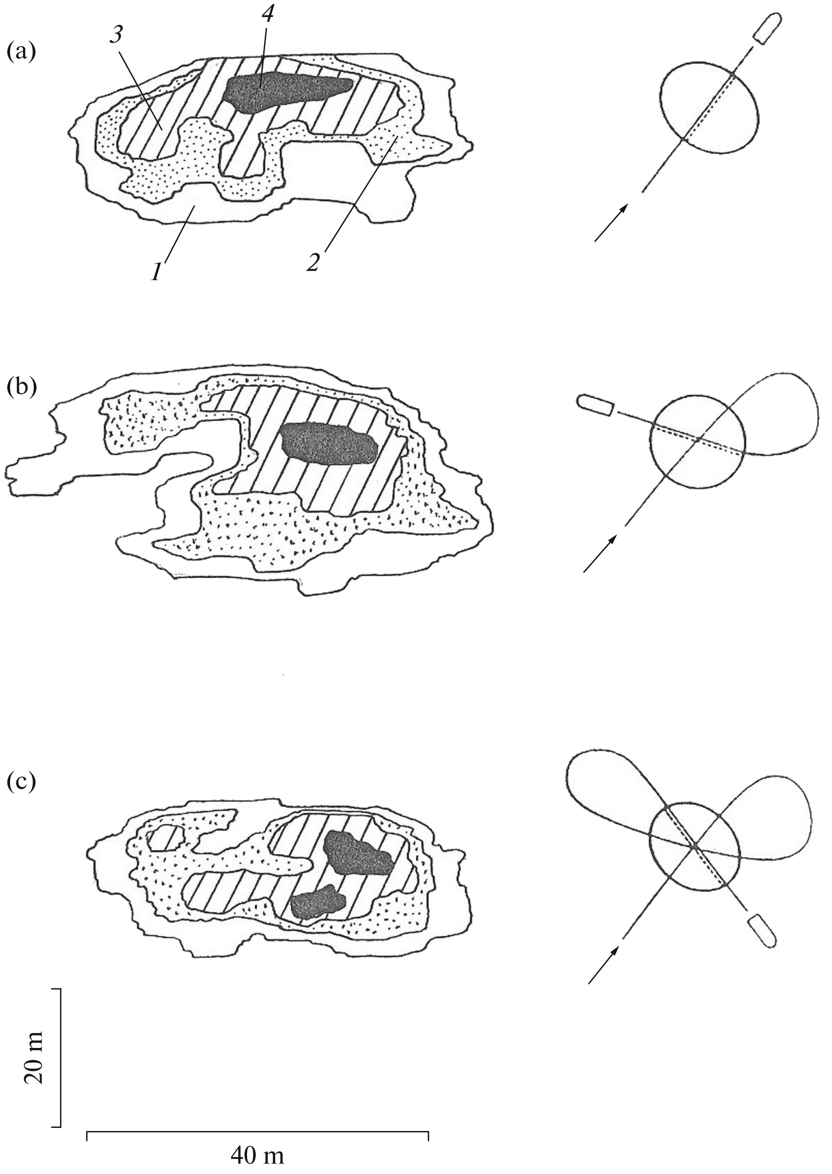

Fig. 12. Fish density in different parts of a school of Atlantic herring *Clupea harengus* estimated using hydroacoustic methods along three transects (a, b, c) with an interval of 3–5 min. The direction of the transects is shown on the right. Fish density, ind./m^3: *1*— 0.1–1.0, *2*—1.0–3.0, *3*—3.0–8.0, *4*—>8.0. The segments indicate the scale (according to: Misund and Floen, 1993).

lengths. Whether fish actively choose a partner of close body size due to visual assessments or whether this choice occurs due to the action of hydrodynamic forces remains unclear (Pitcher et al., 1985). The average density of subgroups is much higher than the average density over an entire school; for example, in capelin schools, the density in subgroups reached 7.60 ind./m^3, while the average for the school was ~0.95 ind./m^3 (Serebrov, 1984). It is believed that individuals in schools and other animals interact most closely with each other precisely within such local intra-school (intra-herd) groupings (Ballerini et al., 2008).

SPATIAL PREFERENCES OF FISH IN SCHOOLS

Fish easily and quickly change their position in schools. The same fish can be located in the front of a school and after a few seconds can be find in the rearguard or on the opposite side of the school with a sharp change in direction of movement (Fig. 15) (Steven, 1959; Kühlmann and Karst, 1967; Reebs, 2001; Leblond and Reebs, 2006; Burns et al., 2012; Krause et al., 2000). Data concerning individual or group preferences of fish to occupy certain positions within a school are scarce. There are observations according to which individuals differing in size are not distributed homogeneously within a school: the average length of

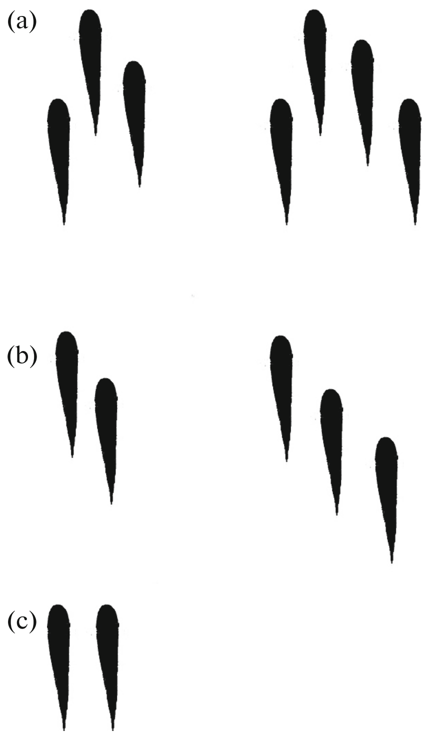

Fig. 13. Mutual arrangement of fish in intra-school subgroups: (a) symmetrical and asymmetrical wedge, (b) ledge, (c) linear arrangement (according to: Zuyev and Belyayev, 1970).

fish from different parts of a school can differ by one third or more (Pitcher et al., 1985; Pitcher and Parrish, 1993). For example, the largest specimens of the Atlantic cod *Gadus morhua* lead schools during their migration to fattening after spawning. Leading fish feed more intensively, their food is more varied and consists of more preferred food items (DeBlois and Rose, 1996). The same regularity was also found in schools of other marine fish—Atlantic mackerel (Pitcher et al., 1982), European pilchard *Sardina pilchardus* (Mužinić, 1977), as well as in schools of underyearlings of common roach *Rutilus rutilus*, in which the relative number of large individuals is higher in front part of schools (Mikheev, 1985). It has also been noted that in schools of considerable thickness, individuals located in the upper layers of the water are smaller than those occupying the lower horizons (Sette, 1950; Breder, 1951; Johnson, 1970).

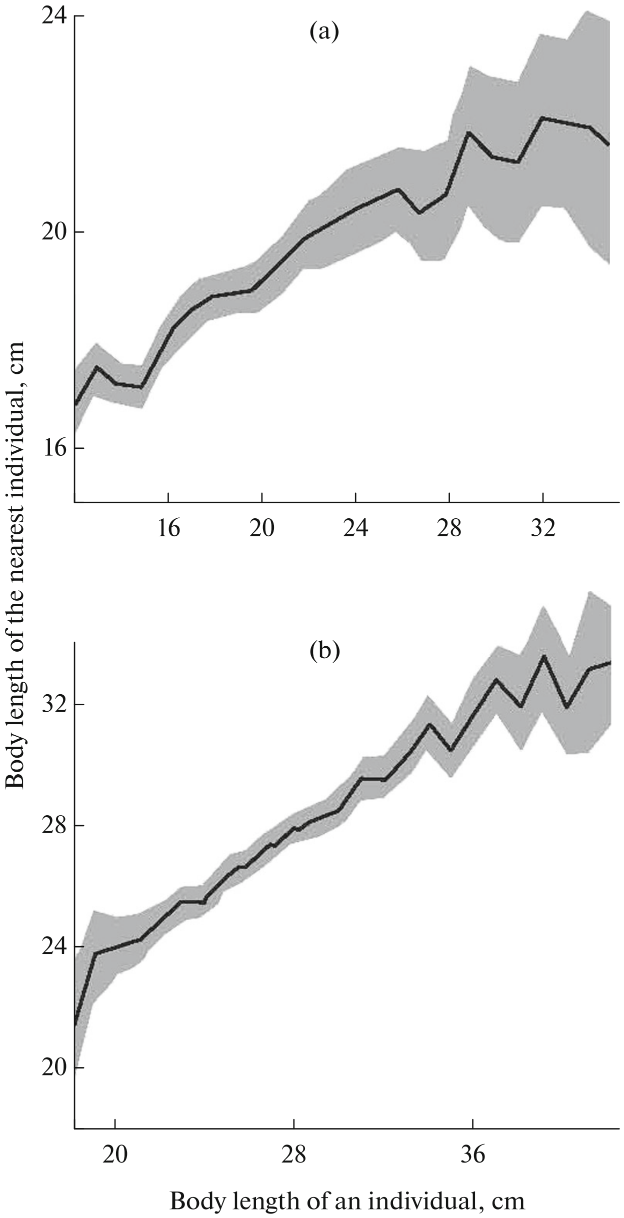

Fig. 14. Correlation between the body length of the closest neighboring fish in schools of Atlantic herring *Clupea harengus* (a) and Atlantic mackerel *Scomber scombrus* (b). The shaded zone is the area of 0.95% confidence intervals (according to: Pitcher et al., 1985).

The location in the school in some cases is associated with the physiological state of an individual. For example, hungry fish are more likely to lead the school (Krause et al., 1992; Krause, 1993). In the schools of the Eurasian minnow, the individuals that have seized the food leave the leadership position, and, as the estimates of the intensity of their metabolism showed, they shift to the back of the school in proportion to the amount of energy that remains after the energy expenditure necessary for the digestion of the prey (a specific dynamic effect of food) and maintaining a standard metabolism—the more food the fish consumed, the higher the energy consumption for digestion, the less energy left for swimming and other activities, and the greater the distance the fish shifted from leadership positions (McLean et al., 2018). These data serve as a good example of the correlation between the physiological state of an individual and its behavior (Krause and Seebacher, 2018). In the golden grey mullet *Chelon auratus*, the individuals in the head of a school are those who are able to more efficiently

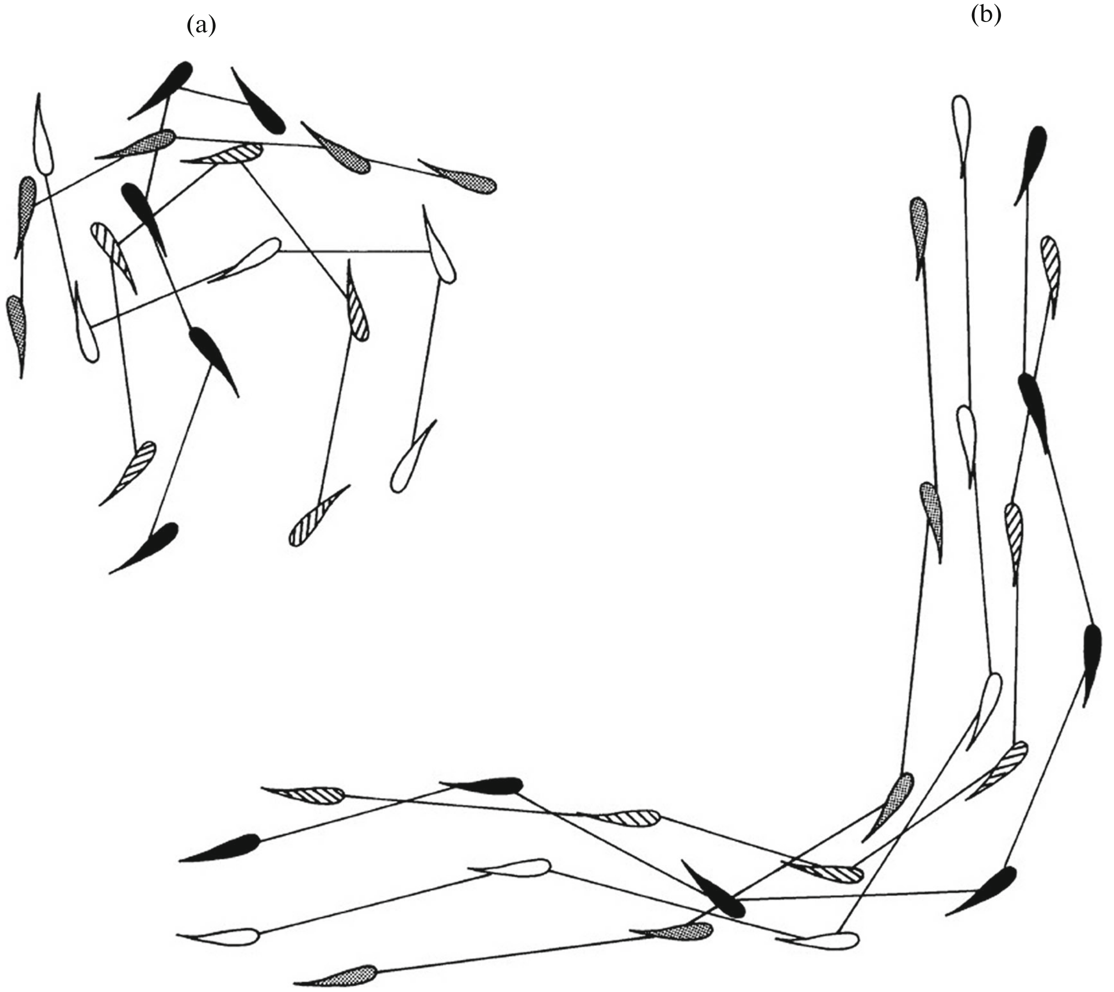

Fig. 15. Individual intra-school trajectories of fish movements during abrupt (a) and calm (b) changes in the direction of movement of a school of the spottail shiner *Notropis hudsonius* (according to Keenleyside, 1979).

extract oxygen from the water and provide a high level of metabolism during physical exercise. With an increase in the speed of movement, fish with a lower metabolic rate prefer to be located in the back of a school, which reduces their energy consumption for swimming (Killen et al., 2011). It has been noted that individuals affected by parasites are usually located on the periphery of a school or at some distance from it, but maintain visual contact with it (Krause and Godin, 1994; Barber et al., 1995). As recently found out, in schools consisting of fish of two different species, individuals of the same species prefer to be located side by side, i.e., the closest partners are often individuals of their own species (Ali et al., 2018).

Individuals in different parts of a school have different benefits and different risks. The position at the head of a school allows the fish not only to feed more intensively, but also increases the likelihood of being attacked by a predator. In specially performed studies that assessed individual spatial preferences in the school and the boldness of an individual—the ability to be the first to leave the shelter or master new conditions, the relationship between leadership and boldness was revealed, but it was not always strongly pronounced (Ward et al., 2004; Leblond and Reebs, 2006). It was also found that in some individuals, leadership is generally stable and manifests itself with obvious constancy in observations made at different times of the day or on different days, which indicates that the intention to be at the head of the school is an internal individual quality of these individuals (Leblond and Reebs, 2006). Individuals in a school also differ in their reactivity—some of them are always the first to react to an external stimulus and drag other partners in a school with them. These individuals are characterized not only by consistently high reactivity, but also by stable spatial preferences (Marras and Domenici, 2013).

However, it is not always possible to reveal the reasons behind the manifestation of intra-school spatial preferences by fish, as, for example, in smolts of the coho salmon *Oncorhynchus kisutch*, in which some individuals preferred to stay at the periphery of a school, while others preferred to stay at the center of a school (Healey and Prieston, 1973). A long-term registration (4 days) of the position of individuals in a school of Atlantic mackerel revealed persistent, lasting throughout the entire observation period, preferences of some individuals to locate in certain places of the school. However, a significant relationship between the body size of fish and their spatial preferences was not found (Pitcher et al., 1982). It is possible that such preferences are more often manifested in artificial conditions, when individuals that form a single school coexist together for a relatively long time and it is possible to form personalized relations between them, up to hierarchical ones. Under natural conditions, when there is a constant regrouping of fish in schools, the breakup of schools and the formation of new ones, the transition of individuals from one school to another, individual spatial preferences of fish are quite likely absent. Under such conditions, only spatial preferences can be observed, determined by the size of fish or their physiological status (food motivation, parasite infestation, etc.) (Krause et al., 1992; Ward et al., 2005; Hansen et al., 2016).

CONCLUSIONS

Thus, schools of fish have a well-defined internal structure, which is rather rigidly determined in a migrating school—in the most striking form of schooling behavior. The ordering of fish in moving schools is expressed not only in the parallel arrangement of individuals, which is easily detected even with simple visual observations, but also in the characteristic displacement of individuals relative to each other, the formation of intra-school groupings, and the intention of fish to settle down next to individuals of close size. The manifestation of the internal organization of schools, their density are clearly related to the size of fish, with their motor capabilities. Many of the structural features of schools are determined by the physical forces that arise when fish swim.

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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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