

Mechanisms of Schooling Behavior of Fish

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Received March 2, 2023; revised April 17, 2023; accepted April 17, 2023

Abstract—The basic mechanisms of schooling behavior of fish, which is a genetically fixed species character, have been considered. The intention of schooling fish to unite with individuals of their own species or with fish that are similar in shape, color and motor activity pattern (schooling reaction) is an innate reflex that manifests itself in natural and artificial environments in individuals with different individual experiences. The intention to unite is expressed the stronger, the more schooling behavior is characteristic of fish. The larger the school, the more attractive it is for fish. To choose a school for association, it is enough that it be 2–3 times larger than the rest. This difference decreases with an increase in the number of fish in schools, with the threat of a predator attack and other stresses. In juveniles, the intention to unite with larger schools is more pronounced than in adult fish. Given a choice, fish prefer individuals of their own species and fish similar in size and color. Imitation is an unconditioned reflex, which is another important mechanism of school behavior. Imitative reactions are most pronounced in schooling fish, but their manifestation is possible if the imitated and imitating fish are conspecific and close in size. An innate optomotor reaction (following reflex) ensures that fish maintain a single school during movements and rapid maneuvering. Schooling coordination is achieved by focusing on the actions of one of the closest partners, and the parallel arrangement of fish is achieved by accurately following the leading partner. Recognition of individuals of their own species, mutual orientation and coordination of actions of fish is facilitated by schooling coloration—spots, stripes and patterns on the body, head and fins, differing in position, size, shape, color, brightness and other details. Important visual landmarks are the contrasting eyes of school partners. Schooling coloration is not present in all schooling fish. In many species, schooling coloration changes as the fish grow and develop.

Keywords: fish, schooling behavior, innate reflexes, schooling reflex, imitative behavior, imitation reflex, optomotor reaction, schooling coloration

DOI: 10.1134/S0032945223070081

Schooling behavior is an innate species property. Like many other genetically fixed characters, school behavior can be subject to natural selection and artificial selection. It is known that the cave (blind) form of the banded astyanax *Astyanax mexicanus* (= *fasciatus*) does not form schools or groups, in contrast to the sighted form that inhabits terrestrial water bodies and exhibits a typically schooling lifestyle (Parzefall, 1983; Gregson and Burt de Perera, 2007). Fish of both forms interbreed easily, and among hybrids it is possible to detect individuals with normally developed eyes and vision, but not showing schooling behavior. From molecular genetic studies, it follows that the loss of schooling in them was the result of relaxed selection, which caused genetic changes in the loci of quantitative characters responsible for the transmission and processing of visual information (Kowalko et al., 2013). Although the data on the time of the formation of the cave form are contradictory, it is believed that the development of cave reservoirs and, accordingly, the loss of schooling took place no more than 3 million

years ago (Wilkins and Strecker, 2017). Changes in the manifestation of schooling in fish, apparently, can occur and be fixed genetically much faster. As shown by the example of the guppy *Poecilia reticulata*, directional breeding already within three generations made it possible to obtain a line whose fish (females) swam in a school with a higher (by 15%) polarization (Kotrschal et al., 2020). Differences in the characteristics of schooling swimming (mutual orientation of individuals, school density, coordination of movements) were found when comparing several dozen lines of zebrafish *Danio rerio* (Tang et al., 2020).

Fish exhibit schooling behavior regardless of their individual experience. Individuals reared in complete isolation from other individuals of their own species or from fish of other species easily form a school and show all signs of schooling swimming (Breder and Halpern, 1946; Shaw, 1960, 1961; Kerr, 1962; Williams, 1976; Köhler, 1988). Larvae of the European bitterling *Rhodeus amarus* begin to swim in a school almost immediately after they leave the mantle cavity

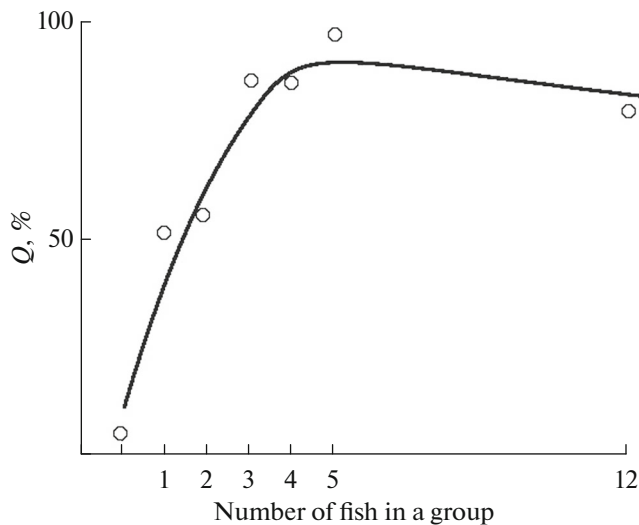


Fig. 1. Intensity of the attraction reaction, shown by a solitary sunbleak *Leucaspius delineatus* in relation to groups with different numbers of individuals. Q —percentage of time that solitary sunbleaks spent at the aquarium wall, behind which there is a group of conspecific individuals (according to: Darkov, 1975).

of the bivalves *Colletopterum cyreum cyreum* (Anadonta) (Pashchenko and Kasumyan, 2017). The strength of the schooling instinct of fish is very great and often dominates over other innate reactions, in particular, defensive ones. For example, schooling fish break through a gas bubble screen that frightens them if they can join the rest of the school in this way (Radakov, 1973). This was shown, in particular, experimentally on the Pacific herring *Clupea pallasii*, which passed through a gas bubble screen imitating a wall of air bubbles created by the humpback whale *Megaptera novaeangliae* when hunting, only if there was another school of herring on the other side. The larger it was, the easier the fish overcame the fear to unite (Sharpe and Dill, 1997). Cases of active entry of solitary fish into a trawl were repeatedly noted if the main part of a fished school was in it at that moment (Korotkov, 1969).

MUTUAL ATTRACTION OF SCHOOLING FISH TO EACH OTHER

Schooling behavior is based on the intention of fish to unite with individuals of their own species or with fish that are close to them in shape, color and features of motor activity. Mutual attraction of schooling fish to each other—schooling reaction, many researchers consider it as the main property of schooling behavior. Very simple, but very illustrative examples of this peculiarity in the behavior of schooling fish are experiments with presenting the fish with their own reflection in a mirror. The schooling feeling is so strong that the fish rarely leave the zone of the aquar-

ium near which the mirror is placed. The more schooling behavior is characteristic of fish of any species, the stronger their positive reaction to their own reflection in the mirror (Spooner, 1931; Aronov, 1967; Darkov, 1980) or to the appearance of fish of their own species (Protasov, 1961).

School Size

The larger the school, the more attractive it is for fish when schooling. Using the example of the sunbleak *Leucaspius delineatus*, it was shown that solitary individuals spend much more time near the transparent wall of the aquarium, behind which they see other individuals of their own species. The attraction reaction occurs even if there is only one individual in the adjacent compartment. If the number of displayed fish is increased, then the attracting effect rapidly increases and ceases to increase significantly when the number of such fish reaches three (Fig. 1) (Darkov, 1975, 1980). In schooling fish—the dace *Leuciscus leuciscus*, the bream *Abramis brama*, the Black Sea red mullet *Mullus barbatus ponticus* and some others, with an increase in the number of individuals in the experimental groups from three to six, a significant increase in the optomotor reaction is observed—following the visual landmark (Pavlov, 1970). Similar data have also been obtained for the sunbleak (Protasov and Altukhov, 1960). The manifestation of schooling behavior in the Eurasian minnow *Phoxinus phoxinus* is observed if the number of fish in the school is more than three (Partridge, 1980). In the rosy bitterling *Rh. ocellatus*, the minimum group size at which stable schooling characteristics are maintained is also three individuals (Kanehiro et al., 1985). Based on the above and some other data, it is believed that the union of three individuals is minimally sufficient to form a grouping that has all the characteristics of a school. In nature, the number of fish schools, as a rule, is always much higher than the minimum number of fish shoals, at which stable characteristics of schooling behavior are maintained (three individuals) (Darkov, 1975; Darkov, 1980; Partridge, 1980; Kanehiro et al., 1985).

In order for fish to show a preference for a larger school of two simultaneously in the field of view, for the sunbleak, it is necessary that the sizes of visually accessible schools differ by at least three times (Table 1) (Darkov, 1980). A solitary angelfish *Pterophyllum scalare* prefers one of the two schools that is at least twice as large, and the preference index at this ratio of school sizes (2 : 1) decreases with an increase in their numbers (Gómez-Laplaza and Gerlai, 2016). However, when frightened, the ability to distinguish between the sizes of schools and choose the larger one from two that are simultaneously in the field of view of a single fish is enhanced. This choice is possible even if small comparable schools of up to 10 individuals differ from each other by four or more fish (Krause et al., 1998).

Table 1. Duration of the attraction reaction ($M \pm m$) shown by a solitary sunbleak *Leucaspius delineatus* in relation to two simultaneously presented groups of conspecific individuals (according to: Darkov, 1980, modified)

Ratio of the number of fish in the presented groups 1 and 2	Duration of the attraction to the group, s	
	1	2
0 : 12	4 ± 1	472 ± 25*
1 : 12	95 ± 20	231 ± 30*
2 : 12	95 ± 16	195 ± 25*
3 : 12	106 ± 26	316 ± 42*
4 : 12	82 ± 13	145 ± 24*
5 : 12	216 ± 11	242 ± 11
6 : 12	245 ± 20	275 ± 22
7 : 12	229 ± 26	264 ± 24
8 : 12	245 ± 20	260 ± 20
9 : 12	275 ± 25	257 ± 24
10 : 12	263 ± 24	287 ± 28
11 : 12	255 ± 9	255 ± 16
13 : 12	237 ± 25	257 ± 26

$M \pm m$ —mean and error of mean; *differences between the duration of reactions of attraction to groups are significant at $p < 0.05$.

The intention to unite with larger schools decreases as the number of individuals in the compared schools increases. Under the threat of a predator attack, the choice of a larger school by fish occurs faster, and the accuracy of the comparative assessment of the size of schools increases (Hager and Helfman, 1991). In juvenile fish, the intention to associate with larger schools is more pronounced, which is supposed to reduce the risk of predation (Pitcher et al., 1986a; Ranta et al., 1992b). It is believed that the intention to associate with a larger school is better expressed in those fish that are more likely to experience a real threat of predation, while the fish spend less time making such a choice (Krause et al., 1998). Apparently, when choosing a larger school, the significant signal for the experimental fish is not the number of individuals in the compared schools, but the linear or volumetric dimensions of the school (its silhouette or the volume it occupies). Undoubtedly, an important factor influencing the choice can be not only the volumetric size of a school, but also its mobility as a whole and the mobility of its members (Gómez-Laplaza, 2006).

Sizes of Fish in Preferred Schools

An important factor influencing the entry of fish into a school is the individual's own linear dimensions and the size of fish in selected schools. Laboratory experiments have shown that when given a choice, fish tend to unite with conspecifics close to them in body length (Ranta and Lindström, 1990; Ranta et al., 1992a, 1992b; Krause and Godin, 1994); often closer in size to each other than more distant partners (Pitcher et al., 1985, 1986b; Theodorakis, 1989;

Krause, 1994). When two groups of the three-spined stickleback *Gasterosteus aculeatus* were placed together, in which the average length of the fish was 4.4 and 5.7 cm, after 3–6 min, a single school divided into two, each of which mainly united either large or small fish (Ranta and Lindström, 1990). Size assortativeness in the formation of schools also occurs under natural conditions—this was found when analyzing the size composition of schools of the juvenile three-spined stickleback caught in the coastal area in such a way that all individuals of the school fell into the catch. It turned out that the variability in body size of individuals within a school is much less than between schools caught in the same place and on the same day (Peuhkuri et al., 1997).

Coloration of Preferred Fish

Of great importance when choosing partners in a school is not only the species or body size, but also the peculiarities of the coloration of fish. In experiments on the sailfin molly *P. latipinna*, it was found that individuals of white or black color prefer to unite with fish of a similar color (McRobert and Bradner, 1998). Significant for fish is not only such a very strong visual stimulus as the color of the body, but also other external signs, weaker and not so clearly visible. For example, for the banded killifish *Fundulus diaphanous*, such a sign is small dark spots on the lateral surface of the body. The spots appear due to the appearance in the muscle tissue of fish of cysts of metacercariae of the parasitic trematode *Crassiphiala bulboglossa*, for which fish serve as intermediate hosts. In the pairwise selection experiment, both the trematode-infested and

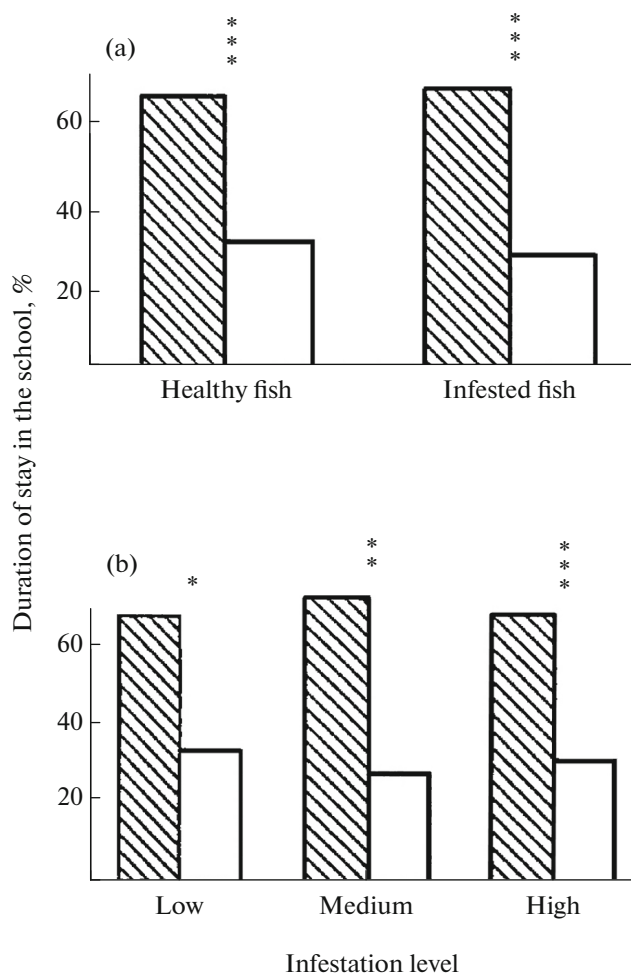


Fig. 2. Duration of stay of the healthy and infested with the trematode *Crassiphiala bulboglossa* striated banded killifish *Fundulus diaphanus* in schools consisting of healthy or infested fish (a), and healthy fish in schools consisting of healthy or infested fish with different severity of invasion (b). Invasion level (number of metacercariae on the fish body), specimens: low—1, medium—2–4, high—≥5. (▨), (□)—schools consisting of healthy and infested fish, respectively. Differences in the duration of stay of fish in schools of healthy and infested killifish are significant at p : * < 0.05, ** < 0.01, *** < 0.001 (according to: Krause and Godin, 1996).

uninfested killifish showed a well-defined significant preference for unspotted uninfested individuals. In the uninfested killifish, the preference was manifested the more clearly, the more infested the fish were, which, simultaneously with the uninfested fish, were presented to experimental individuals for choice (Fig. 2) (Krause and Godin, 1996). The lower attractiveness of infested individuals during schooling was confirmed in similar experiments on other fish species: at pairwise choice, the three-spined stickleback prefers to unite with healthy individuals of its species and avoids those infested with the ectoparasite *Argulus canadensis* (Dugatkin et al., 1994).

Gender of Preferred Fish

Preferences for joining a school may be specific for females and males of fish. For example, male zebrafish prefer to associate with schools of females but not males, or with mixed-sex schools. In females, no such differences in preferences were found (Ruhl and McRobert, 2005).

Familiar and Unfamiliar Preferred Fish

Fish can visually distinguish unfamiliar individuals of their species from familiar ones and show a more pronounced preference for the latter (Ward et al., 2020). This ability has been found, in particular, in various freshwater fish. Preferences for grouping with familiar individuals were found in the three-spined stickleback (Van Havre and FitzGerald, 1988), the bluegill *Lepomis macrochirus* (Brown and Colgan, 1986), the fathead minnow *Pimephales promelas* (Brown and Smith, 1994), and the guppies (Magurran et al., 1994; Lachlan et al., 1998), the Texas shiner *Notropis amabilis*, and the blacktail shiner *Cyprinella venusta* (Farmer et al., 2004). Similar results were also obtained in experiments on the Eurasian minnow: when experimental fish caught in remote places of a river were introduced, joint schools were formed in which the proportion of “familiar” individuals, i.e., caught in one place of the river, reached 75%. Demonstration to fish of a visual model of a predator, the pike *Esox lucius*, did not significantly affect the choice of school partners by fish (Griffiths, 1997). However, in coral fish (*Neopomacentrus azysron*, *Chromis viridis*, *Caesio teres*), the choice between a school consisting of conspecifics and a mixed school did not appear when imitating the presence of a predator (Quattrini et al., 2018).

The discovery of this ability necessitated a more detailed study of the “familiarity effect.” To do this, from a large group of three-spined sticklebacks caught in nature, individuals were taken, equal in size and without the presence of parasites and other individual external features. The fish selected in this way were divided into eight groups of 12 individuals, provided with group marks, and kept in different aquariums for 6 weeks. Then the fish of the two groups were put together and immediately transferred to a large aquarium, in which two usually unequal groups formed already after ~10 min. An analysis of the composition of these groups showed that the division of individuals is statistically different from random, and most often familiar fish dominate in numbers (Barber and Ruxton, 2000). In other experiments, we compared the choice by single minnows of one of two schools simultaneously presented to them, equal in number and composed of familiar (14 days of joint keeping) or unfamiliar individuals. The choice of a school from familiar individuals was observed in all six experiments ($p < 0.05$). At a successive increase in the difference in

numbers between the schools presented for selection, the preference for a school of unfamiliar individuals occurred only if its number was four times higher. But if both schools were composed of unfamiliar individuals, then preference was given to the school, the number of which exceeded only 1.9 times (Fig. 3) (Barber and Wright, 2001). Equally interesting are the results, which show that the zebrafish show a preference for individuals that have the same coloration as those with which the tested fish were reared. At the same time, their own type of coloration did not influence the choice (Engeszer et al., 2004; Spence and Smith, 2007). It has been suggested that this choice may be based on visual imprinting, although the presence of a genetic component is not excluded (Spence and Smith, 2007). The zebrafish reared in isolation showed equal preference not only for their own species, but also for fish of a closely related species, the pearl danio *D. albolineatus*, and even for guppies far from them (McCann and Matthews, 1974).

Despite the fact that most data confirm the preference of fish to school with familiar individuals, there are also examples where such a preference is not found, including in previously studied fish species. For example, it has been confirmed that zebrafish males prefer to associate with other males of their species than to remain alone, but they do not show any selectivity towards familiar males when compared with unfamiliar ones (Blonder and Tarvin, 2022). There are other examples that do not support the higher attractiveness of familiar conspecifics. The inconsistency of the data can be associated, for example, with the different social ranks of the responding individuals and individuals in the chosen schools (Frommen et al., 2007; Gómez-Laplaza and Fuente, 2007). Discrepancies can also be caused by differences in the methods used, different duration of “acquaintance” of experimental individuals, their condition or degree of schooling, and other features of the biology of the studied species. Thus, juveniles of the banded killifish after 18 days of joint keeping in aquariums showed a well-pronounced preference for familiar individuals in the alternative choice, while no such preference was found in schooling juveniles of the bluegill of the same size and with the same experimental procedure. It is assumed that these differences are due to the fact that schooling in the killifish persists throughout subsequent ontogeny, but is lost in the bluegill, which passes to territoriality in adulthood (Lee-Jenkins and Godin, 2010). Evidence is emerging that indicates the influence of the food consumed by them and the odor background on the choice of fish (Ward et al., 2004, 2005; Webster et al., 2007).

The fact draws attention that the ability of fish, when uniting, to give preference to familiar individuals has been confirmed so far only in laboratory conditions using the example of small shoals. Whether this effect manifests itself in the formation of schools of fish in nature remains unclear.

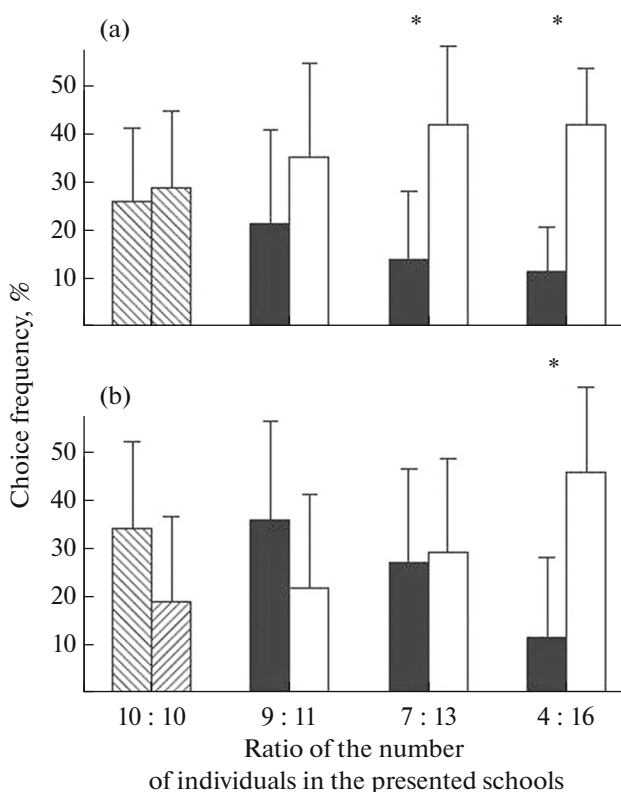


Fig. 3. Average value of the frequency of choice by a solitary Eurasian minnow *Phoxinus phoxinus* of one of two simultaneously presented schools: a—smaller (■), larger (□) and equal in size (▨) schools composed of unfamiliar individuals; b—smaller (■) and larger (□) schools composed of familiar and unfamiliar individuals, respectively; (▨), (▩)—schools equal in size, composed of familiar and unfamiliar individuals, respectively. (I)—standard deviation; * differences in the choice of presented schools are significant at $p < 0.05$ (according to: Barber and Wright, 2001).

There is evidence that fish may prefer closely related individuals (three-spined stickleback) when schooling (Frommen and Bakker, 2004). However, these results have not been confirmed by genetic analysis of individuals belonging to the same wild-caught school (Bernhardt et al., 2012). It is important that the degree of preference shown by schooling fish to conspecifics can be expressed to different extents in individuals of different populations. For example, in the marine form of the three-spined stickleback, this ability is manifested much stronger, as well as the intention to navigate in a school parallel to each other, than in the freshwater benthivorous stickleback form. Population differences in the behavior of marine and freshwater sticklebacks are heritable (Wark et al., 2011).

Thus, the mutual attraction of fish to each other is the main mechanism leading to the association of fish in schools. The schooling reaction is an innate reflex that dominates over many other genetically deter-

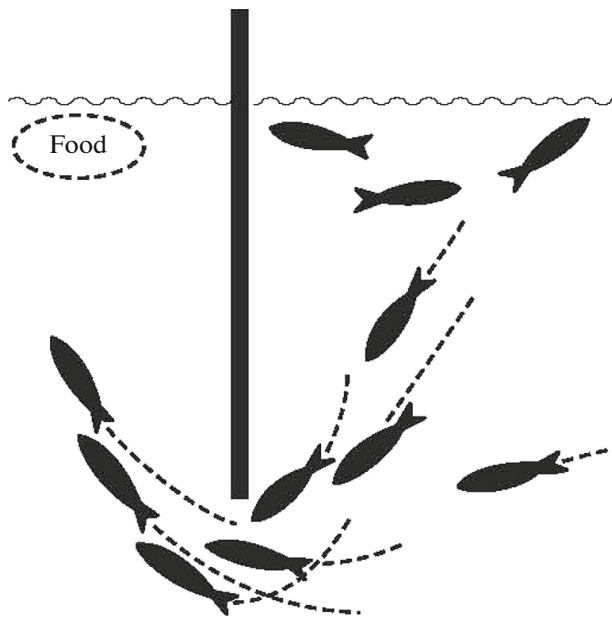


Fig. 4. Detection by a fish school of food separated by an opaque partition (according to: Radakov, 1973).

mined reactions of fish, but is realized under the influence of individual experience and the state of the individual and environmental conditions. The intention to unite is expressed the stronger, the more schooling behavior is characteristic of fish, while such characters as the size and number of fish, the shape of their body, physiological state, coloration features, the presence of a threat from predators, and others are essential.

IMITATIVE BEHAVIOR

Imitation is an unconditioned reflex, which consists in the repetition of behavioral actions by some individuals ("spectators") after others ("actors") whom they observe. This ability is an essential element in the behavior of schooling fish. It is in schooling fish that imitative reactions are most pronounced, while fish leading a solitary lifestyle, such as, for example, the shorthorn sculpin *Myoxocephalus scorpius*, the viviparous eelpout *Zoarces viviparus*, the rock gunnel *Pholis gunnellus* (Gerasimov, 1983), or sturgeon fish (Acipenseridae) (Sbikin, 1996), do not manifest these reactions. The beginning of manifestation of the ability to imitate coincides in fish ontogeny with the transition of juveniles to school swimming (Leshcheva, 1968; Volkova, 1976; Leshcheva and Zhuikov, 1989).

Imitation is of great importance in the life of schooling fish. Thanks to well-developed imitative behavior, the unity of a school is maintained when moving and when performing complex and fast maneuvers when frightened or in response to a predator attack. The role of imitation in the behavior of schooling fish is well demonstrated by experiments performed on the juvenile haddock *Melanogrammus*

aeglefinus in aquariums partially separated by an opaque partition (Fig. 4). The food that was brought into one of the compartments of the aquarium could be noticed only by individuals located in the same compartment. The fish swimming in the neighboring compartment did not see the food, but they could see the rapid burst of other fish to the food, which caused them to quickly move to the opposite compartment. Soon almost all experimental fish gathered in the compartment with food. The same situation is observed when only a part of the fish detects and is the first to directly react to an attacking predator or another frightening stimulus; after them, all the other fish show a defensive reaction and the school as a whole moves away from danger (Verheijen, 1956; Milanovskii and Rekubratskii, 1960; Radakov, 1973). The transition of remaining members of a school to the feeding zone is not observed when the food is distributed diffusely, and not aggregated. In this case, all members of the school are in equal conditions in terms of food supply and do not react to each other (Ryer and Olla, 1995), which is in good agreement with observations of a feeding school, when fish temporarily lose their common orientation and are randomly distributed within food spot.

Imitating fish not only imitate the behavior of other fish, but also quickly learn the same skills that actor fish (demonstrators) have, i.e., acquire conditioned reflexes from other individuals, being only witnesses to the actions of the latter. Undoubtedly, the acquisition of conditioned reflexes from other fish is biologically more beneficial than the development of these reflexes on the basis of one's own experience. Non-hereditary transmission of information from individual to individual or from generation to generation is called signaling continuity (Lobashev, 1967; Manteifel', 1987). For example, in order to develop a conditioned reflex to the wels catfish *Silurus glanis*, a single and short-term observation of the successful hunting of this predator is enough for the sunbleak (Girsa, 1981). In other experiments, the sunbleak acted as a predator, feeding on the juveniles of the common roach *Rutilus rutilus* in the aquarium. Roach juveniles, which themselves were not attacked by a predator, but only saw its successful hunting for other juveniles, also developed a strong defensive reflex to a predator (Popov, 1953). For schooling fish, the possibility of developing imitation reflexes not only of the first order, but also of the second and third orders was shown, when the skills acquired by spectator fish are successively adopted by other fish (Leshcheva and Zhuikov, 1989). The more actor fish demonstrate a certain skill, the more successfully it is transferred to spectator fish that do not possess it, but stay with the actor fish in the same school (Laland and Williams, 1997; Lachlan et al., 1998).

Conditioned imitation reflexes in fish are developed to stimuli of very different nature (Bogomolova et al., 1958; Leshcheva and Zhuikov, 1989) and are

characterized by rapid formation and high stability. Thus, in the Atlantic cod *Gadus morhua* and in the saithe *Pollachius virens*, a conditioned reflex in the form of a directed motor reaction to irritation with an electric current is manifested in a spectator individual already at the first combination of this stimulus and a motor-defensive reaction demonstrated by an actor individual. For the haddock, such combinations, on average, required somewhat more. Imitating individuals not only repeat the escape of actor fish to another compartment, but are also able to imitate more subtle features of their motor response, for example, short sharp movements to the side at the first moment of exposure to an electric current. The developed conditioned imitation reflexes to light and acoustic stimuli do not show noticeable extinction even after 200 or more trials. One individual can stimulate the manifestation of an imitative reaction in a shoal consisting of spectator fish up to 9 ind. (Gerasimov, 1983).

The manifestation of an unconditioned imitation reflex and the formation of conditioned imitation reflexes are possible only if the imitated and imitating fish belong to the same species and are close in size. The Atlantic cod and the saithe did not imitate individuals of their own species, if the sizes of the fish participating in the experiment differed by only 20%. There is no imitation if different species of similarly sized fish (the Atlantic cod and the haddock) are used as actor and spectator fish. This feature can be considered as one of the main mechanisms for the formation of monospecies schools consisting of individuals of similar size. Imitative behavior is also not manifested in relation to individuals of their own species, in which the coordination of movements is disturbed (Gerasimov, 1983). Imitation is much less pronounced in solitary fish than in schooling ones (Rekubratskii, 1967).

OPTOMOTOR RESPONSE

The optomotor reaction, which is a compensatory motor reaction in response to a change of the position of visual landmarks in space, is the main mechanism of fish orientation in the water flow. It also plays an important role in manifesting schooling behavior by fish (Breder, 1959; Protasov and Altukhov, 1960; Dambach, 1963; Shaw and Tucker, 1965; Pavlov, 1970, 1979). In schooling fish, neighboring individuals serve as visual reference points for the manifestation of a compensatory motor reaction. The following reflex ensures the preservation of a single school by fish in reservoirs with currents and with stagnant water.

The important role of the optomotor reaction in schooling behavior is emphasized by the fact that this reaction is most pronounced in schooling fish, such as, for example, the South big-scale sand smelt *Atherina boyeri*, the European anchovy *Engraulis encrasicolus*, and juveniles of most fishes. This reaction is noticeably enhanced in the presence of individuals of

their own species, which is apparently achieved due to the imitative behavior developed in fish. The compensatory motor reaction to the movement of visual landmarks in the field of view is also characteristic of non-schooling fish leading a solitary lifestyle, but it is less pronounced in them. Moving figures of various shapes, netting, fish models can serve as schooling landmarks for fish. Kozarovitskii (1961) singled out the movement following after outwardly most similar animals as a special reaction and called it the following reflex. However, specially conducted experiments showed that this reflex is only a special case of an optomotor reaction—a reflex of following moving visual landmarks. It was found that visual identification of the presented images or objects, their exact resemblance to the appearance of the fish themselves is not necessary. Fish follow just as readily the objects (squares, rectangles, circles) that do not even remotely resemble the silhouettes of reacting fish (Pavlov, 1970). Despite the fact that the optomotor reaction seems to be of some importance in maintaining contacts between individuals within a school, the following reflex cannot play a leading role in ensuring school behavior (Pavlov, 1970, 1979). This is also indicated by the significantly earlier formation of the optomotor reaction in fish ontogeny than that of schooling behavior (Masuda and Tsukamoto, 1996).

INTRA-SCHOOL INTERACTIONS

The regularities of intra-school interactions of fish, which provide a common orientation of individuals, rapid dissemination of information, and coordinated movements of an entire school, still attract much attention of researchers. The main methodological approach that makes it possible to obtain important data concerning this problem remains the observation and video recording of schooling swimming of fish, followed by a detailed and comprehensive tracking of the position and trajectory of movements of individuals. The use of just such a method makes it possible to discover new features of schooling swimming. It turned out that when moving in a school, fish (eastern mosquitofish *Gambusia holbrooki*) do not swim monotonously, but constantly change their speed of movement (Herbert-Read et al., 2011). They either speed up swimming if the distance to the fish swimming behind is reduced to less than two body lengths, then they slow down the movement if they come close to the individual swimming in the front. An analysis of video materials also revealed that the parallel arrangement of fish in a school is most likely achieved not due to orientation towards a partner swimming nearby, but due to a clear following of the individual swimming in the front (Fig. 5). The above authors believe that the schooling coordination of the actions of fish occurs due to the orientation towards the actions of not many, but, apparently, only one of the closest partners in the school.

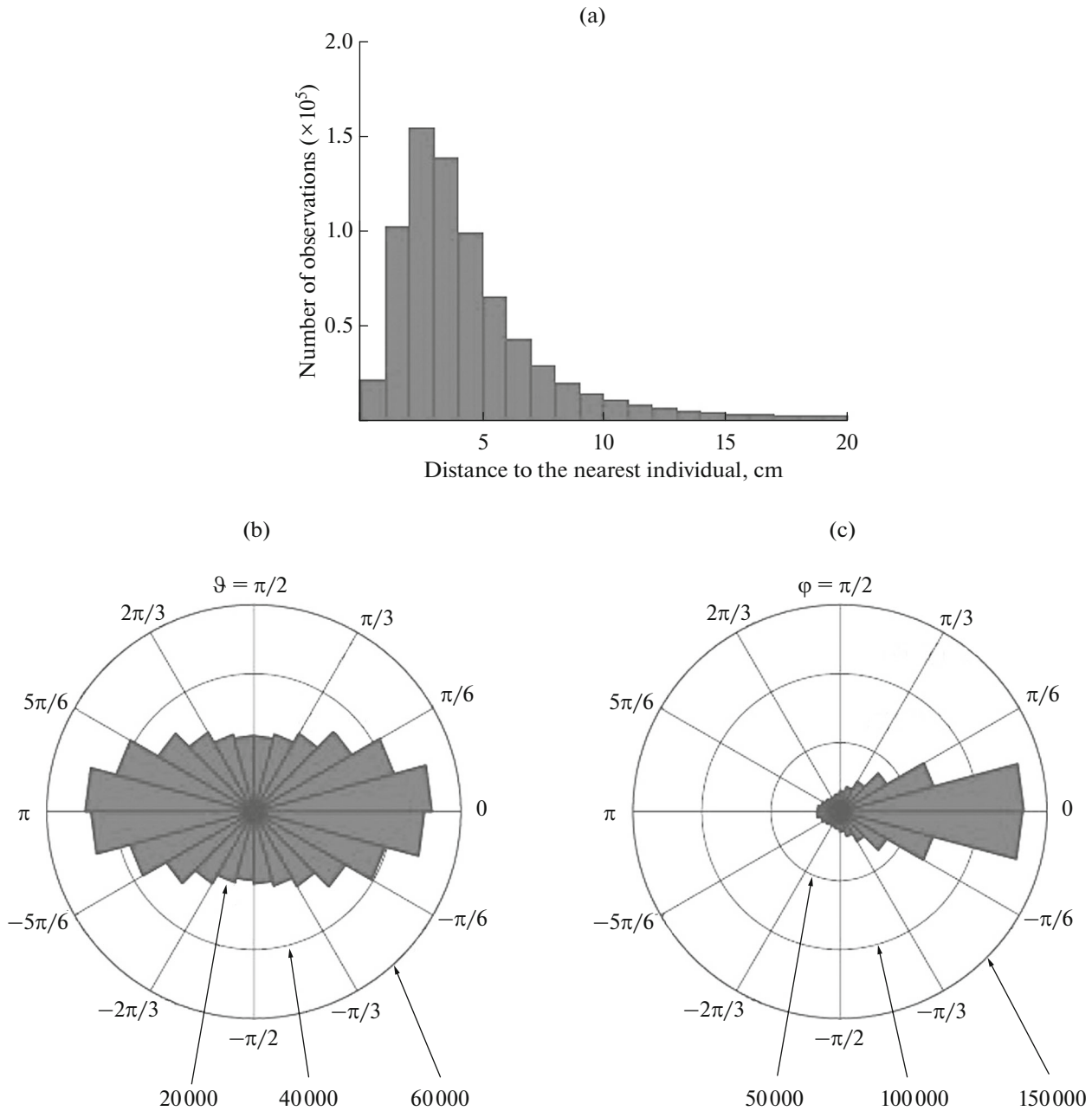


Fig. 5. Location of the mosquitofish *Gambusia holbrooki* in a school (according to data obtained from frame-by-frame analysis of video recordings of the position of individuals in a school of ~ 50 fish for 5 min; shooting speed is 15 frames per second). Frequency distribution: a—distances from the focal individual to the nearest partner, b—location of the nearest partner relative to the focal individual (ϑ); c—orientation of the body of the nearest partner relative to the focal individual (φ). The arrows show the number of observations on the frequency scale (according to: Herbert-Read et al., 2011).

Similar results were also obtained as a result of another study (Katz et al., 2011), the purpose of which was to search for patterns that govern the interactions of schooling fish with each other. The work was carried out independently and almost simultaneously with the previous one, but on a different fish species, the golden shiner *Notemigonus crysoleucas*. High-speed and high-resolution video recording was used to analyze the speed and trajectory of movements of

individuals in a school and to assess the dependence of these parameters on the actions of neighboring fish. It was found that the golden shiner in a school maintains a certain distance to the nearest partner ~ 1.5 – 2.0 body length, but not less than one and not more than four body lengths, in the sector from -60° to 60° . Monotonous swimming, as well as for the mosquitofish, is completely uncharacteristic for them, the movements of the shiner are a constant alternation of accelerations

and decelerations of the swimming velocity. Like the mosquitofish, the golden shiner speeds up swimming when an individual swimming behind it approaches it and slows it down if the fish swimming in the front is in close proximity to it. In other words, the velocity of a fish is determined by the location (distance) of a fish swimming directly in the front and behind, while the distance to a fish located on the side does not affect the swimming velocity. The authors come to the conclusion that swimming velocity is the main component of the regulation of intra-school interactions and the location of fish in a school.

As in the mosquitofish, the coaxiality (parallelism) of the arrangement of the golden shiner in a school is achieved due to the orientation towards a partner swimming in the front, but not towards a partner located behind. At the same time, the higher the swimming velocity of fish, the stricter the coaxiality of fish. The coherence of the response of fish is ensured by imitation of the actions of partners in a school, and the imitation of the actions of one of them (interaction between pairs) has the greatest contribution, although the actions of other partners can determine the average reaction of an individual (Katz et al., 2011). It is important that with an increase in the size of a school, the swimming velocity of fish decreases, and the distance to the nearest neighbor increases (Middlemiss et al., 2018).

Other than speed, important regulators of intra-school interactions are turns, i.e., deviations of fish from a rectilinear swimming trajectory. If fish located one after another in a ledge are separated by a small distance, within the same body length, then the tendency (probability) to turn in a lagging fish is small. But as this distance increases, i.e., the farther forward and to the side the fish went, the probability of making a turn in the same direction for the fish swimming behind increases. In other words, the change in the direction of swimming of the fish, its departure to the left or right, in contrast to the swimming velocity, depends on the position of the lateral neighbor in a school, and not on the one located in the front or behind (Katz et al., 2011). It is interesting that in schools that are heterogeneous in species composition, the closest partners are often conspecifics, but the distance to the nearest partner is maintained the same regardless of what species it belongs to and whether these fish had a previous historical experience of cohabitation (Ali et al., 2018).

COLORING OF SCHOOLING FISH AND ITS SIGNAL SIGNIFICANCE

Schooling behavior is provided due to the ability of fish to perceive and respond to visual stimuli, the source of which are partners in a school. Such stimuli, along with the shape and size of the fish body, include coloration. Many schooling fish have a special type of coloration, which is commonly called schooling col-

oration. Schooling coloration is characterized by the presence of contrasting spots, stripes or characteristic patterns on the body, head or fins of fish. These visual landmarks in fish of different species differ not only in location, but also in size, shape, color, brightness, and other details. The presence of such visual markers facilitates the recognition of individuals of their own species, mutual orientation and coordination of fish during schooling swimming.

Bright, clearly visible spots or stripes are found on the body or fins of many schooling fish. For example, the haddock has a dark contrasting spot on the front of the body next to the pectoral fin. The European perch *Perca fluviatilis*, which is a facultative schooling fish, has a bright black spot on the front of the dorsal fin. Dark spots, one or more, are found on the body or fins of many other schooling fish, for example, the Far Eastern sardine *Sardinops sagax*, the European pilchard *Sardina pilchardus*, the Caspian shad *Alosa caspia*, the Eurasian minnow, the teardrop butterflyfish *Chaetodon unimaculatus*, the four-eyed butterfly fish *Ch. capistratus*. The characteristic external attributes of many schooling fish are contrasting stripes, which can be located on the body both in the longitudinal and transverse directions. Such stripes, different in length, width, shape or pattern, are found in mackerel (*Scomber* spp.), bonito (*Sarda* spp.), some tuna (*Thunnini*); in many representatives of cardinal fishes (Apogonidae)—the large-toothed cardinalfish *Cheilodipterus macrodon*, the oblique-banded cardinalfish *Apogon semiornatus* and the five-lined cardinalfish *C. quinquelineatus* and others; carangids (Carangidae) — the pilot fish *Naucrates ductor*, the doublespotted queenfish *Scomberoides lysan* and others; silversides (Atherinidae), in schooling characinids (Characiformes)—penguin fishes (*Thayeria* spp.), pencil fish (*Nannostomus* spp.), tetras (*Hemigrammus* spp.), neons from the genera *Hyphessobrycon* and *Cheirodon*, headstanders (*Chilodus* spp.) and many other species (Fig. 6). Pattern features that create dark stripes on the body of fish are often used by researchers not only for species recognition, but also for individual recognition of experimental individuals (Pitcher et al., 1982). Many schooling fish have both stripes and dark spots on their bodies; for example, juvenile minnows have not only a black spot at the base of the caudal fin, but also a dark stripe along the entire lateral surface of the body (Soin et al., 1981). In some schooling fish, for example, in the Atlantic mackerel *S. scombrus* and in tuna, dark stripes and spots on the body, numerous and varied in shape and size, form a complex pattern, which is a characteristic signal feature used for recognition and mutual orientation by these fast-swimming schooling fish (Fig. 7).

Some fish show mimicry, taking on the coloration of other schooling fish, which allows them to unite with them in joint schools. The juveniles of the poisonous blackline fangblenny *Meiacanthus nigrolineatus* living in the coastal zone of the Red Sea, with a

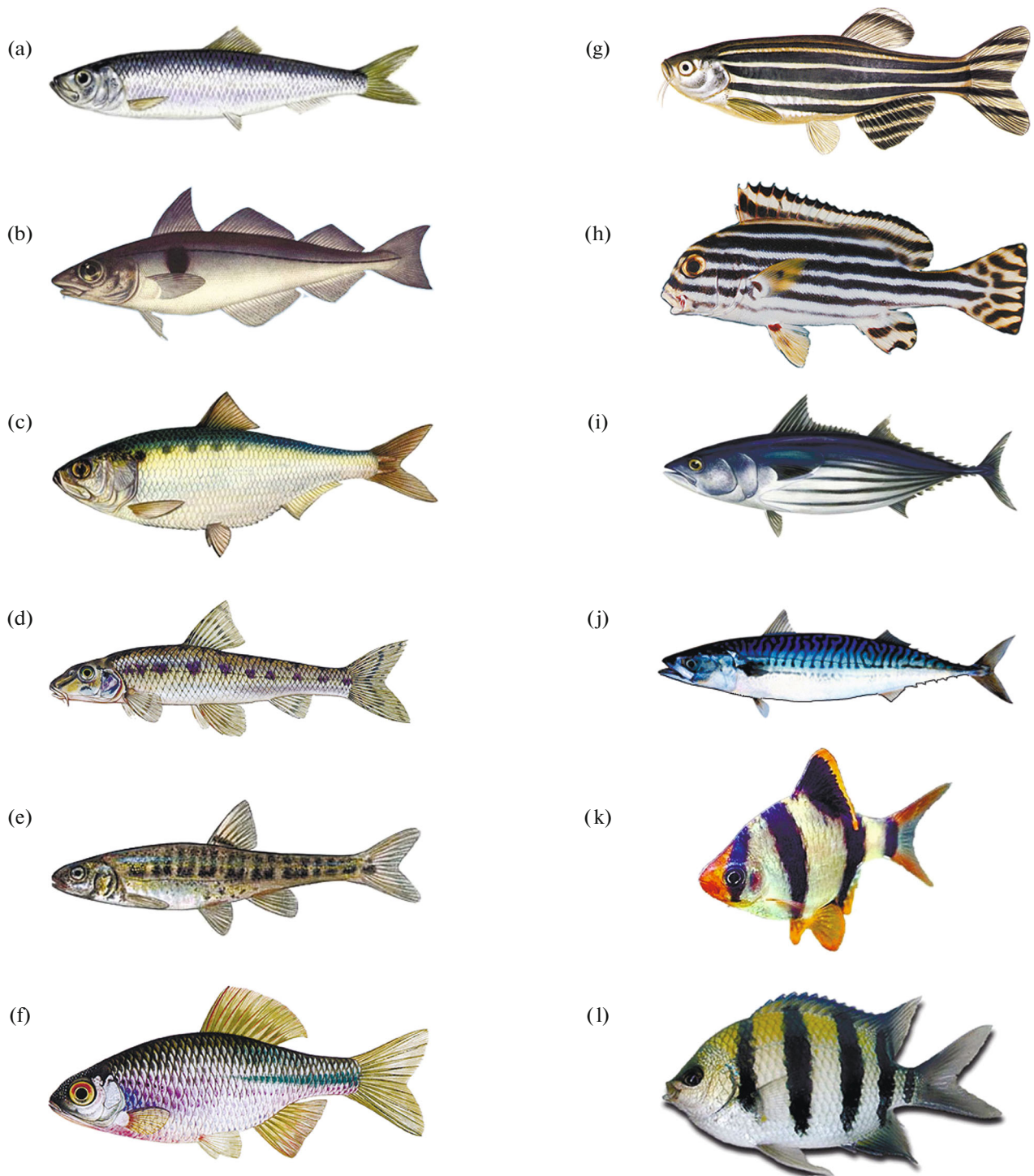


Fig. 6. Examples of coloration of schooling fish: a—Atlantic herring *Clupea harengus*, b—haddock *Melanogrammus aeglefinus*, c—Caspian shad *Alosa caspia*, d—gudgeon *Gobio gobio*, e—Eurasian minnow *Phoxinus phoxinus*, f—European bitterling *Rhodeus amarus*, g—zebrafish *Danio rerio*, h—oriental sweetlips *Plectorhinchus vittatus*, i—Atlantic bonito *Sarda sarda*, j—Atlantic mackerel *Scomber scombrus*, k—tiger barb *Barbus (=Puntigrus) tetrazona*, l—Indo-Pacific sergeant *Abudefduf vaigiensis*.

body length of <20 mm, are practically indistinguishable from many species of cardinal fishes (Apogonidae) and live in their schools. However, when the length is >30 mm, the juveniles begin to acquire the coloration of adult fish, different from that of cardinal

fishes, and leave their schools (Dafni and Diamant, 1984). The juvenile Cherskii's thicklip gudgeon *Sarcocheilichthys cherskii* has a dark oblong stripe along the entire body and, until a certain age, keeps in schools of juveniles of other fish species, such as the Amur min-

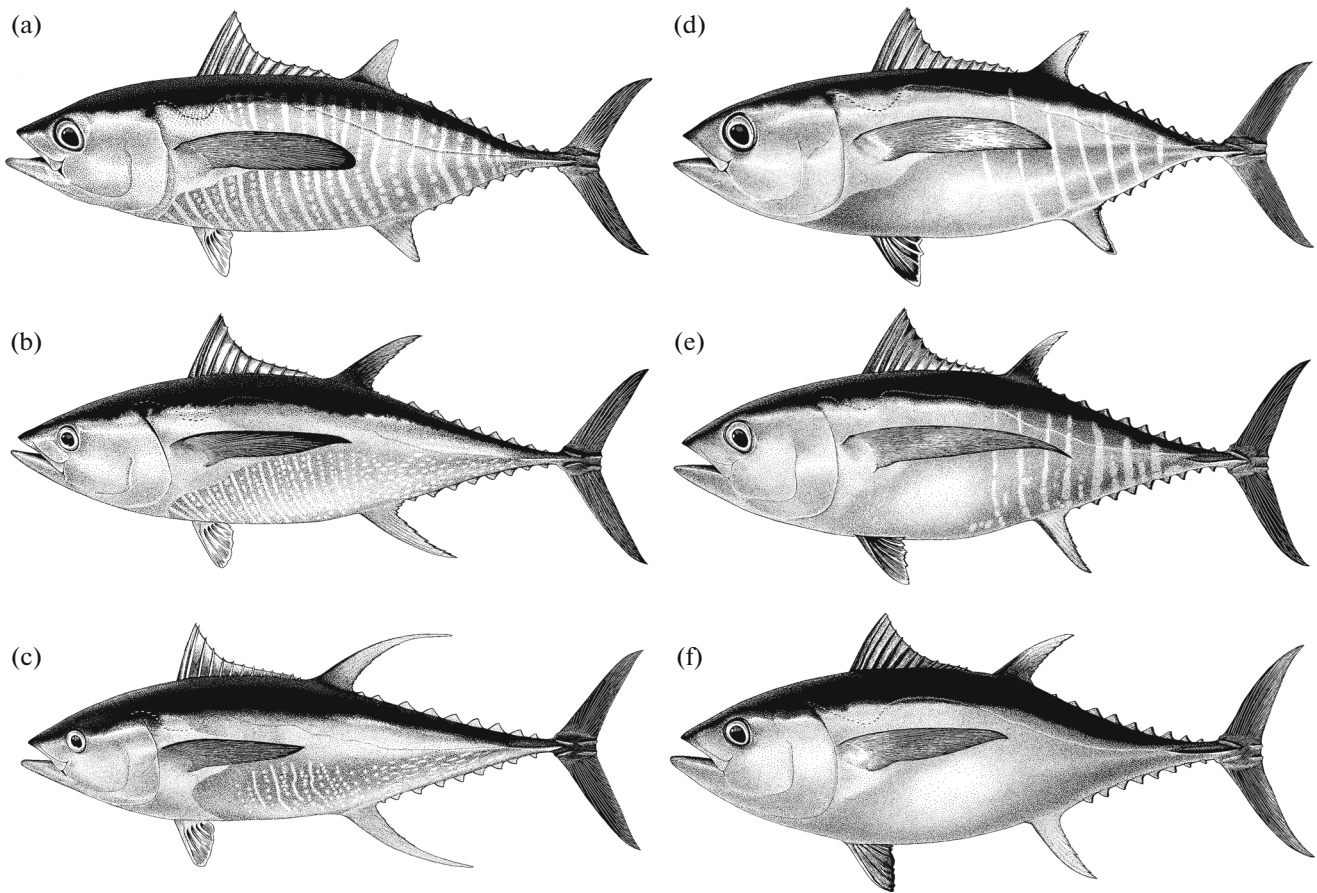


Fig. 7. Coloration change with growth in the yellowfin (*Thunnus albacares*) (a–c) and the bigeye (*Th. obesus*) (d–f) tunas. Body length, cm: a, d—~40; b, e—~80; c, f—~130 (according to: Schaefer, 1999).

now *Rhynchocypris lagowskii* or the stone moroko *Pseudorasbora parva* (Nikol'skii, 1974). There are other interesting examples of school coloration mimicry (Dafni and Diamant, 1984; Pereira et al., 2011).

The importance of schooling coloration in the life of fish is emphasized by the fact that it is enhanced in those conditions when schooling behavior becomes especially important, for example, when there is a potential threat of a predator attack. The smell of pike, which is a natural chemical danger signal for small cyprinids (Cyprinidae), causes not only a defensive reaction in the Eurasian minnow (leaving, hiding), but also leads to the appearance of a contrasting black stripe on the lateral surface of the fish (Lebedeva and Chernyakov, 1978; Malyukina et al., 1980). Some fish are able to quickly, within minutes and even seconds, change color depending on the situation or behavior. Thus, the juvenile parrotfish *Chlorurus sordidus* has several different types of coloration that it takes on when swimming in a school. Two of them are characteristic of smaller juveniles, and these types of coloration (monotonously dark coloration and striped) are not specific and are inherent in juveniles and other coral fish. The third type of coloration (ocellated) is

typical for larger individuals, which can be found more often alone than in a school (Fig. 8). The color change from one type to another occurs quickly, within seconds (Crook, 1997).

Schooling coloration does not remain constant during ontogeny and in many species it changes as the fish grow and develop. For example, late larvae and early juvenile of the Eurasian minnow have a clearly visible continuous dark pigment stripe on the sides and a black spot at the base or in the center of the caudal fin. In an adult minnow, the dark stripe on the sides is transformed into a series of wide dark spots with blurred outlines, and the pigment spot on the caudal fin disappears (Fig. 9) (Soin et al., 1981). Larvae of the crucian carp *Carassius carassius* have a small accumulation of pigment cells on the caudal peduncle at the base of the caudal fin, which in early juvenile transforms into a black vertically elongated spot. The spot persists throughout the first year of life, but then, as juveniles grow, it becomes less noticeable and gradually completely disappears. In the closely related goldfish *C. gibelio*, such a spot is absent throughout the entire ontogeny (Dmitrieva, 1957; Koblitskaya, 1981).

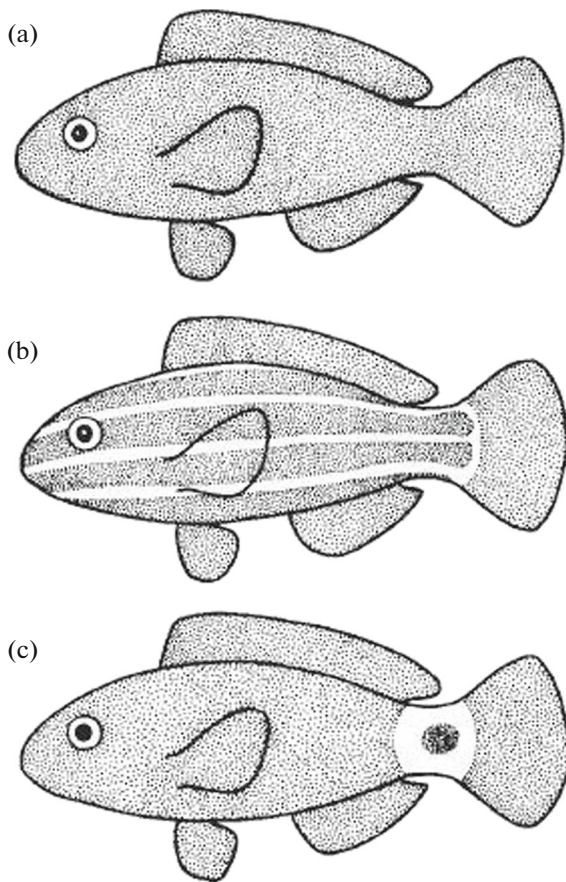


Fig. 8. Different types of coloration of the juvenile parrotfish *Chlorurus sordidus*: a—monotonously dark (non-specific), b—striped (non-specific), c—ocellated (specific for this species) (according to: Crook, 1997).

In the Russian bitterling *Acanthorhodeus* (= *Acheilognathus*) *asmussi*, the larvae and juvenile show typical schooling behavior, they are characterized by the presence of a bright black spot on the dorsal fin. With age, these fish begin to lead a solitary lifestyle, and the spot on their dorsal fin is lost (Fig. 9) (Nikol'skii, 1974). Quite significant changes in schooling color with the growth of fish occur in tuna. In the bigeye tuna *Thunnus obesus*, body length according to Smith ~40 cm, on the sides, starting from the middle of the body, there are large and rare vertical light stripes, which in larger fish begin to break up into spots, small light rounded spots appear between the stripes. But in large individuals of the bigeye tuna (~130 cm), the stripes and spots completely disappear. In the yellowfin tuna, coloration is different, but, like in the bigeye tuna, it is also much more complex in smaller individuals than in large fish (Fig. 7) (Schaefer, 1999).

However, not all schooling fish species have a well-defined schooling coloration in the form of spots, stripes or patterns on the body or fins. For example, many species of herring fish (Clupeidae), which, after undergoing metamorphosis, lead an exclusively

schooling lifestyle, do not have any characteristic features in color—representatives of the genera *Clupea*, *Sprattus*, *Clupeonella*. There are also no specific color features in many schooling cyprinids, such as the sunbleak, the common bleak *Alburnus alburnus*, the dace and others. For these fish, an important visual stimulus that ensures the attraction of fish to each other and their mutual orientation in a school can be silver body color or contrasting black eyes. In the experiment of the white bream *Blicca bjoerkna*, in 75% of cases, it shows a positive reaction to models painted in silver and only in 25%—in white or black (Herter, 1953). The silver-colored models also have an attractive effect on the sunbleak (Darkov, 1980). In the process of smoltification, juvenile salmonids (Salmonidae) acquire a silvery coloration of the body, passing from a territorial way of life to schooling behavior in preparation for the migration from rivers to the sea (*Pacific salmon ...*, 1991). It cannot be ruled out that spots and stripes that are invisible in schooling fish under ordinary light will appear in them in the ultraviolet (UV) spectrum, as was found in some coral reef fish (Losey et al., 1999). The rapid attenuation of the UV component of light (320–400 nm) in water does not limit the use of such visual signals for close communication (Lythgoe, 1968; Siebeck and Marshall, 2001; Siebeck et al., 2010), corresponding to the distance of intra-school contacts of fish.

The importance of visual stimuli outcoming from other partners in the school is evidenced by observations made on the Atlantic cod (Chinarina, 1959). These fish change body color not under the influence of the color of the surrounding background, but, first of all, in accordance with the color of other fish in a school or the color of a model: on a white background, the experimental fish are dark in color if other fish next to them are also dark in color, or if a dark-colored model is presented. Due to this feature, the unification of all fish in the school is achieved, which is of great importance not only for the implementation of the actual schooling behavior, but also reduces the vulnerability of fish when encountering a predator (Chinarina, 1971).

The function of visual landmarks is also performed by other external signs of fish, for example, the size and shape of the body, and even the nature of swimming. Zebrafish spend a longer time near striped models, and it is important that the size of the model and the size of the experimental fish match (Breder and Halpern, 1946; McCann et al., 1971). The Atlantic silverside *Menidia menidia* does not accept individuals of its own species into a school if their size exceeds the average size of fish in the school by more than 50% (Shaw, 1962). An important role of behavioral features (motor activity), coloration, size, and body shape of fish as factors influencing the process of school formation was also established in experiments on other fish species (Keenleyside, 1955; Darkov, 1980).

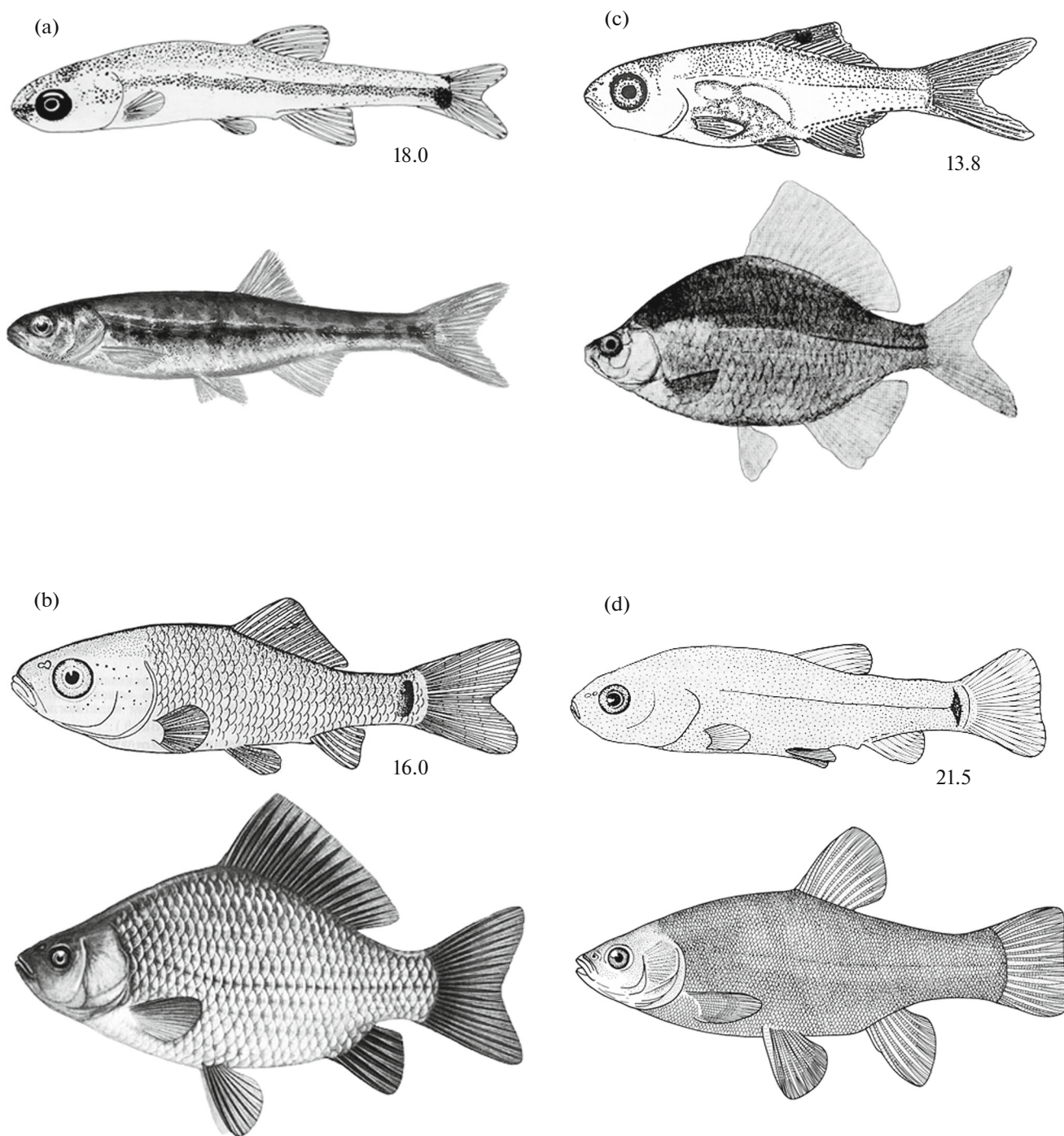


Fig. 9. Age-related changes in coloration in cyprinids: a—Eurasian minnow *Phoxinus phoxinus* (according to: Pinder, 2001), b—crucian carp *Carassius carassius* (according to: Dmitrieva, 1957), c—Russian bitterling *Acanthorhodeus* (= *Acheilognathus*) *asmussii* (according to: Soin, 1978), d—tench *Tinca tinca* (according to: Koblitckaya, 1981). Juveniles and sexually mature individuals are depicted; for juveniles, the standard length in cm is indicated.

Like other characters, the coloration of schooling fish can change during evolution due to changes in living conditions. Examination of found fossils of *Mene rhombea*, aged ~48 million years, has shown that these now extinct fish had contrasting dark stripes on the body, while the modern representatives of the same

genus, *M. maculata*, have small dark spots on the body, mostly elongated vertically (Fig. 10). It is believed that the extinct *M. rhombea* were pelagic fish, unlike *M. maculata*, living in the sea near the bottom and feeding mainly on benthos (Froese and Pauly, 2022; Rossi et al., 2022).

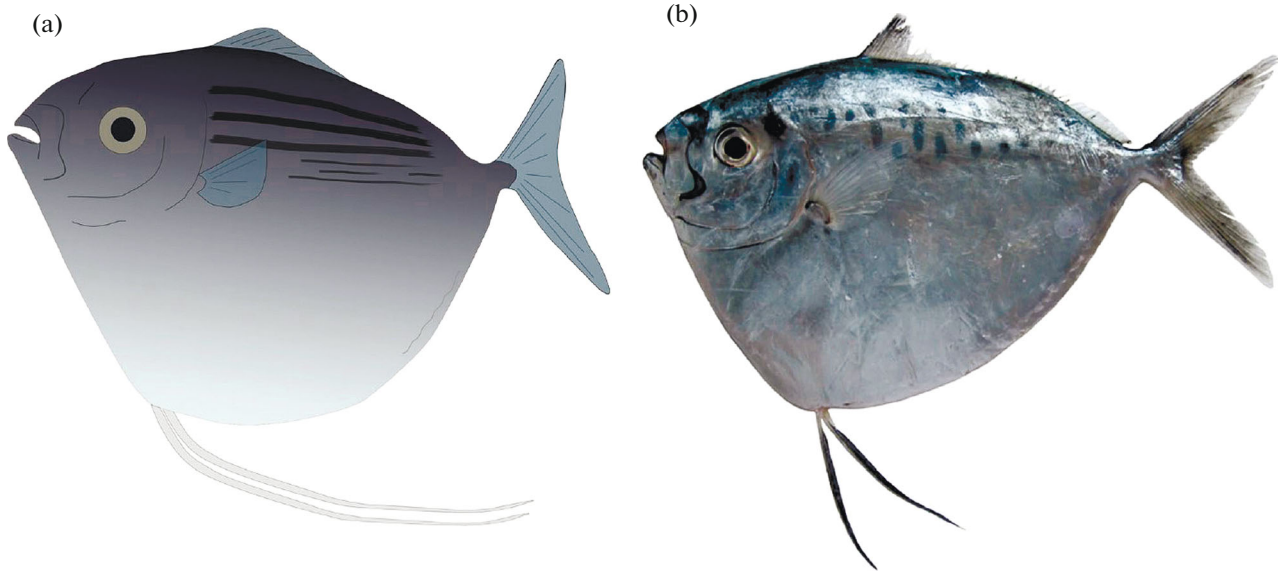


Fig. 10. Reconstruction of the coloration of the extinct *Mene rhombea* (based on fossil remains, age 48 million years) (a) and the coloration of the living moonfish *M. maculata* (b) (according to: Rossi et al., 2022).

Visual stimuli outcoming from partners in a school, primarily the color and shape of the body, are important stimuli for the rest of the fish in the school. These stimuli have a signal value and serve as a source of information about the position of individuals in the school, their behavior, they contribute to the mutual coordination and coordination of the actions of schooling fish.

The great importance of spots, stripes, patterns and other characteristic features in coloration for schooling fish does not raise any doubts. For a schooling behavior, which is almost completely determined by vision, such stimuli are certainly important for recognition, selection, and association with representatives of their own species, and facilitate mutual orientation and coordinated schooling swimming. The importance of schooling coloration is emphasized by mimicry, which allows some species to enter schools of other fish, by the strengthening of schooling coloration when danger occurs or when a certain age is reached. It should be emphasized that the presence of spots and stripes on the body and any other noticeable features in the coloration is not an external sign that the fish belong to schooling species. There are a large number of fish that have such characteristics, but do not show schooling behavior, and lead, as a rule, a group and/or territorial way of life. In these fish, coloration also performs important signaling functions, but associated with the maintenance of dominant–subordinate relations in the group, protection of their own territory, and other behavioral features.

CONCLUSIONS

Thus, the mechanisms of schooling behavior that ensure the association of fish, their mutual orientation, and coordination of movements are well studied. The innate nature of schooling behavior is convincingly shown, which, however, can manifest itself to varying degrees and depend on many external factors and on the condition of fish. The most important quality of schooling fish is the ability to imitate, which not only saves a school during sharp and fast maneuvering, but also ensures the rapid development and transfer of new skills. The role of the optomotor reaction in intra-school contacts has not yet received due experimental consideration. In the last few years, a certain progress has been observed in the study of intra-school interactions of fish, associated with the use of accurate recording equipment and detailed data analysis. This made it possible to obtain important information about the mechanisms that determine the consistency and interdependence of the movements of individuals in a school and their maintenance of a uniform orientation. Undoubtedly, this methodological approach will make it possible to elucidate new basic patterns of schooling swimming.

ACKNOWLEDGMENTS

The authors express their sincere gratitude to A.A. Kazhlaev, L.S. Alekseeva, and A.S. Patseva (Moscow State University), who provided great assistance in preparing the article for publication. The authors are sincerely grateful to P.I. Kirillov (Institute of Ecology and Evolution, Russian Academy of Sciences) for careful and constructive editing of the text and illustrations, which improved the quality of the article.

FUNDING

The article was prepared within the framework of scientific projects of the state assignment of the Moscow State University No. 121032300100-5 and the Institute of Ecology and Evolution, Russian Academy of Sciences No. 121122300056-3 in the Unified State Information System for Accounting the Results of Civil Research, Development and Technological Works.

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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Translated by S. Avodkova

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