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Comparative Analysis of Taste Preferences in Fishes with Different Ecology and Feeding

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Abstract—Taste preferences four classical taste substances and 21 free amino acids in seven fish species are assessed by the behavioral method: roach *Rutilus rutilus*, goldfish *Carassius auratus gibelio*, guppy *Poecilia reticulata*, cichlasoma *Heros* (*Cichlasoma*) *severum*, nine-spined stickleback *Pungitius lupus*, arctic flounder *Liopsetta glacialis*, and the common wolffish *Anarhichas lupus*. Comparative analysis of the data along with extensive information from the literature supported high species specificity of the taste spectra of the fish studied. No relationship was found between the environmental conditions (water salinity) and the taste preferences of the fish to salts and other taste stimuli. It was shown that fish species with a pronounced herbal component (roach, guppy) have a positive response to sucrose. The relationship between the frequency of snaps of the food item and the duration of its retention in the oral cavity (retention time) was studied in relation to the attractiveness of the item.

Feeding in fish significantly differs at various stages of the life cycle, in various seasons of the year, during long migrations, etc. The range of food objects depends on the environment, physiological and motivation state of the fish, and their age and behavior.

Using adequate food objects, assessment by fish of taste properties of the prey and its agreement with the food requirements significantly depend on the functioning of the taste system (Atema, 1980; Pavlov and Kasumyan, 1990, 1998). Many studies of this sensory system have been made mainly on morphological characteristics and topography of taste buds, their cellular organization and innervation, and the structure of taste centers (Kapoor *et al.*, 1975; Reutter, 1986; Jakubowski and Whitear, 1990; Kanwal and Finger, 1992). Analysis of functional parameters of the taste system was in many cases conducted with electrophysiological methods (Marui and Caprio, 1992), whereas the data on the response of the fish to the taste of various substances are limited and scarce. Comparative analysis of these results was for a very long time difficult or impossible because of the diversity of methods and approaches used by various investigators for the assessment of taste preferences in fish. The development and application of the standard method for the assessment of taste preferences (Kasumyan and Sidorov, 1992, 1994) recently allowed to reveal certain patterns of fish responses to taste stimuli of various type. It revealed a high level of species specificity of the taste spectra of attractive or aversive substances (Kasumyan, 1997). However, many aspects of this important problem, associated with fundamental questions of trophology and ecology of fish and the choice of adequate food objects still remain poorly studied. The relationships between taste preferences and the width of the food spectrum, the composition of the consumed food organisms, and individual food experience are almost completely unclear. The data on the behavioral taste response in fish with varying ecology and life style are very limited. The aim of the present work was comparison of taste preferences and characteristics of the behavioral taste response in fish with different feeding patterns living in waters with different hydrochemical (salinity) or hydrological (current) parameters.

MATERIALS AND METHODS

The objects of the study were seven fish species: two-year-old roach *Rutilus rutilus* (nine specimens) with a length of 6.5 cm (here and in sequel, we present the total length, TL), underyearlings of the goldfish *Carassius auratus gibelio* with a length of 6.5 cm (nine specimens), adult guppy *Poecilia reticulata* aged 6–8 months and the length 2.5 cm in length (20 specimens), juvenile cichlasoma *Heros* (*Cichlasoma*) *severum* aged 4–5 months 6 cm in length (13 specimens), yearlings of the nine-spined stickleback *Pungitius lupus* 4.8 cm long (ten specimens), juvenile arctic flounder *Liopsetta glacialis* aged 6 months 6.3 cm long (seven specimens), and juvenile common wolffish *Anarhichas lupus* aged 5–6 months 7.8 cm in length (nine specimens). Roach were caught in Zvenigorod near Moscow, goldfish were brought from the Russian Federal Research and Production Company on Fish

Culture (Dmitrov, Moscow oblast), and guppies and cichlasoma were bought in pet stores. Nine-spined sticklebacks were caught in the River Khimka (Forest Pokrovskoye-Glebovo, Moscow), and arctic flounders were caught in Kandalaksha Gulf of the White Sea (Velikaya Salma Strait). The young of the wolffish was reared artificially from eggs obtained from spawners, caught in the same region of the White Sea.

The fish were acclimated to aquarium conditions from two weeks to several months. During this time, they were kept in common aquaria at optimal for each species temperatures. The fish were fed daily with live or frozen Chironomid larvae or cod (*Gadus morphua*) meat (arctic flounder and wolffish). One to two weeks before the experiment, the fish were kept individually in small aquaria (5 to 12 l depending on the fish size). The back and side walls of these aquaria were opaque, for visual isolation of the fish. Observations were conducted through the transparent frontal wall of the aquarium. Experiments on the arctic flounder and common wolffish were conducted in a stream-water chute-like apparatus, divided into 25 l compartments. The sea water consecutively passed all compartments along the main axis of the apparatus.

Before the experiment, during several days, the fish were trained to take artificial food pellets made of agar-agar, which contained food extracts (75 g/l). Then, we began assessment of taste preferences of the fish to various substances, free amino acids (L-stereo isomers) and classical taste substances, causing the basic types of taste sensations in humans (the list of the taste substances used and their concentrations are given in Table 1). During the experiment, a food pellet with certain taste substance was transferred into the aquarium. With the pellet having been taken by the fish, we measured (1) whether the pellet was eaten or rejected by the fish, (2) the number of snaps, (3) the retention time of the pellet after the first snap and (4) the total retention time during the experiment. The moment of swallowing of the pellet was determined by termination of characteristic chewing movements by jaws and return to rhythmic movements of the gill covers. The retention time was recorded using *Agat* stop watches. Pellets with different substances were presented to the fish in random sequence. Pellets with taste substances were altered with pellets containing food extracts. Experiments in which the fish did not take the pellet within one minute were dropped. In experiments with the wolffish, the methods were different: in the experiment, individual fish were presented with ten agar-agar plates ($4 \times 4 \times 2$ mm) containing certain tested taste substances. After one minute, we counted the number of the remaining plates, which were then removed from the aquarium. The interval between tests on the same fish in all experiments was at least 10–15 min. The pellets were cut out from agar-agar gel immediately before the experiment.

To prepare the gel, agar-agar powder (Reanal, 2%) was dissolved in hot water and the solution was mixed with the solution of the tested substances or chironomid extract. To make the pellets more conspicuous, we stained the gel: green (Cr_2O_3 0.35, in experiments with cichlasoma or wolffish) or bright red (Ponceau 4R, 0.0005 M, in experiments with other fishes). In experiments with the roach, guppy, and nine-spined sticklebacks, the pellets were 1.5 mm in diameter and 2.5 mm in length. In experiments with the goldfish and arctic flounder, 2.0 and 3.0 mm, respectively. In control experiments, we used pellets containing only the stain. Gel with amino acids or classical taste substances was kept at +5°C not more than 7–10 days. Gel with food extract was kept under the same conditions not more than 3–4 days.

Statistical analysis of the results included computation of the chi-square test, *t*-test, and Spearman rank correlation coefficient (r_s). In total, 13500 experiments were conducted.

RESULTS AND DISCUSSION

Taste Preferences

The results of the assessment of taste preferences in seven species studied to four classical taste substances and 21 free amino acids are given in Table 1. Comparative analysis of these results reveals significant differences in the consumption of the pellets with the same substance by different fish species. One aim of this study was analysis of the patterns of taste preferences in fishes inhabiting waters with different salinity. Out of the seven species studied, the following were freshwater: roach, goldfish, guppy, and cichlasoma. The marine fishes included the arctic flounder and the common wolffish. The nine-spined stickleback is a euryhaline species, inhabiting freshwater and sea water habitats. The most interesting is the comparison of taste responses of these fishes to pellets with sodium chloride and calcium chloride, which are very important components of natural waters. In the Kandalaksha Gulf, where the arctic flounder and the wolffish live, and where the experiments with these fishes were conducted, the content of Na^+ is about 8 g/kg; Ca^{++}, 0.3 g/kg; and Cl^-, 15 g/kg (Bruevich, 1960). The salinity of the White Sea water ranges from 20–24‰ in the nearshore and 10–15‰ near the estuaries to 30‰ at significant depths (Berezina, 1984). In the freshwater water bodies of the Moscow region, where the roach, goldfish, and the nine-spined stickleback were caught, the content of ions is much lower: the concentration of Na^+ varies from 5.3 to 12.5 mg/l; Ca^{+-}, from 0.2 to 69.74 mg/l; and Cl^-, from 4.9 to 11.4 mg/l (Drachev, 1968; Khomchenko, 1991). Cichlasoma and guppy inhabit tropical waters of south America, where the content of Na^+ is 2–3 mg/l; Ca^{++}, 5.4 mg/l; and Cl^-, 2.6 mg/l (Khomchenko, 1991).

Table 1. Consumption (P %, $M \pm m$) of pellets with classical taste substances and free amino acids (L-stereoisomers) by fish

No.	Stimulus	Concentration, M	Roach		Goldfish		Guppy		Arctic flounder		Nine-spined stickleback		Common wolffish		Cichlasoma	
			P, %	n	P, %	n	P, %	n	P, %	n	P, %	n	P, %	n	P, %	n
	Classical taste substances															
1	citric acid	0.26	0**	29	37.5 ± 6.1***	64	31.7 ± 4.7***	101	60.2 ± 5.0*	98	78.9 ± 4.7***	76	15.0 ± 3.2*	127	21.0 ± 2.4**	291
2	calcium chloride	0.9	57.7 ± 9.9	26	53.3 ± 6.5*	60	2.0 ± 1.4	100	86.7 ± 3.4	98	12.7 ± 3.8	79	11.4 ± 2.9	123	50.7 ± 3.0***	272
3	sodium chloride	1.73	73.1 ± 8.9*	26	51.6 ± 6.4*	62	1.0 ± 1.0	101	90.8 ± 2.9*	98	12.7 ± 3.8	78	12.5 ± 3.0	120	5.1 ± 1.3***	279
4	sucrose	0.29	73.1 ± 8.9*	26	74.0 ± 5.5	65	45.5 ± 5.0***	101	78.6 ± 4.2	98	15.6 ± 4.2	77	6.4 ± 2.1	141	25.0 ± 2.6	268
	Free amino acids															
5	alanine	0.1	65.7 ± 8.1**	35	60.0 ± 7.8	40	0	101	87.5 ± 4.2	69	–		–		–	
6	arginine	0.1	74.3 ± 7.5***	35	73.2 ± 7.0**	41	0	100	85.7 ± 4.2	70	–		–		–	
7	asparagine	0.1	38.9 ± 8.2	36	23.8 ± 6.7	42	0	100	85.7 ± 4.2	70	–		–		–	
8	asparagic acid	0.01	13.5 ± 5.7	37	64.3 ± 7.5	42	1.0 ± 1.0	101	92.6 ± 3.2	70	–		–		–	
9	valine	0.1	41.7 ± 8.3	36	81.0 ± 6.1***	42	1.0 ± 1.0	100	92.9 ± 3.1	70	–		–		–	
10	histidine	0.1	33.3 ± 8.0	36	22.5 ± 6.7	40	0	100	88.6 ± 3.8	70	–		–		–	
11	glycine	0.1	51.6 ± 9.1	31	90.5 ± 4.6***	42	92.1 ± 2.7***	101	85.7 ± 4.2	70	–		–		–	
12	glutamine	0.1	58.3 ± 8.3*	36	21.4 ± 6.4	42	42.0 ± 5.0***	100	87.5 ± 4.2	70	–		–		–	
13	glutamic acid	0.01	33.3 ± 8.0	36	50.0 ± 9.0	32	50.0 ± 5.0***	100	82.9 ± 4.5	70	–		–		–	
14	isoleucin	0.01	19.4 ± 6.7	36	85.4 ± 5.6***	41	0	100	85.7 ± 4.2	70	–		–		–	
15	leucin	0.01	44.4 ± 8.4	36	97.4 ± 2.6***	39	0	100	85.7 ± 4.2	70	–		–		–	
16	lysine	0.1	45.7 ± 8.5	35	23.5 ± 7.4	34	8.0 ± 2.7*	100	75.7 ± 5.2	70	–		–		–	
17	methionine	0.1	38.2 ± 8.5	34	20.0 ± 6.4	40	0	100	85.7 ± 4.2	70	–		–		–	
18	norvaline	0.1	62.2 ± 8.1**	37	23.8 ± 6.7	42	1.0 ± 1.0	100	85.7 ± 4.2	70	–		–		–	
19	proline	0.1	31.6 ± 7.6	38	10.8 ± 5.2**	37	3.0 ± 1.7	100	85.7 ± 4.2	70	–		–		–	
20	serine	0.1	77.8 ± 7.0***	36	72.5 ± 7.1**	40	0	100	85.7 ± 4.2	70	–		–		–	
21	tyrosine	0.001	55.6 ± 8.4*	36	93.2 ± 3.8***	44	0	100	81.4 ± 4.7	70	–		–		–	
22	threonine	0.1	69.4 ± 7.8***	36	88.6 ± 4.8***	44	0	101	91.4 ± 3.4	70	–		–		–	
23	tryptopfan	0.01	60.0 ± 8.4*	35	32.5 ± 7.5	40	1.0 ± 1.0	100	85.7 ± 4.2	70	–		–		–	
24	phenylalanine	0.1	28.6 ± 7.7	35	17.5 ± 6.1*	40	0	100	85.7 ± 4.2	70	–		–		–	
25	cysteine	0.1	20.0 ± 6.9	35	38.4 ± 7.9	39	7.9 ± 2.7*	101	80.0 ± 4.8	70	–		–		–	
	Bloodworms extract															
26	series 1	75 g/l	82.8 ± 7.1**	29	95.5 ± 2.5***	67	93.1 ± 2.2***	131	100***	98	91.1 ± 2.0***	214	83.3 ± 3.1***	144	89.3 ± 2.1***	207
27	series 2	75 g/l	97.7 ± 2.3***	43	97.6 ± 1.7***	83	93.1 ± 2.5***	102	100***	98	–		–		–	
	Control															
28	series 1	–	37.0 ± 9.5	27	71.2 ± 5.9	59	2.0 ± 1.4	100	75.5 ± 4.4	98	15.8 ± 4.2	76	6.0 ± 2.2	117	32.8 ± 3.0	244
29	series 2	–	28.6 ± 7.1	42	42.5 ± 7.9	40	1.0 ± 1.0	100	81.4 ± 4.7	70	–		–		–	

Note: The significance of differences from the control: * $p < 0.05$; ** $p < 0.01$, *** $p < 0.001$. Series 1 and 2 were conducted in experiments with classical taste substances and free amino acids, respectively.

It was found that sodium chloride is a taste stimulant (increasing the consumption of the pellets) for the arctic flounder and the roach. In the wolffish, the guppy, and the nine-spined stickleback, the response to pellets with sodium chloride is indifferent. For goldfish and cichlasoma, this salt is a deterrent substance, i.e., it significantly reduces the consumption of pellets. Calcium chloride is a taste stimulator only for cichlasoma. All other fish respond indifferently to it (Table 1).

The absence of a clear relationship between the hydrochemical characteristics of the environment (salinity) and the response of the fish to the taste of sodium chloride and calcium chloride support the data from the literature. Such freshwater fishes as dace *Leuciscus leuciscus*, tench *Tinca tinca*, grass carp *Ctenopharyngodon idella*, lake trout *Salvelinus namaycush*, and anadromous Caspian trout *Salmo trutta caspicus* are characterized by a stimulating effect of sodium chloride. In freshwater Siberian sturgeon *Acipenser baeri*, anadromous starred sturgeon *A. stellatus*, and marine navaga *Eleginus navaga*, this salt causes significant reduction in pellet consumption (Kasumyan and Sidorov, 1993; Kasumyan and Kazhlayev, 1993; Kasumyan and Sidorov, 1995a; Kasumyan and Morsi, 1996, 1997; Kasumyan, 1997, 1999; Kasumyan and Prokopova, 2001). From the same literature sources, it is known that calcium chloride increases the consumption of the pellets in the carp, tench, chub *Leuciscus cephalus*, lake trout, rainbow trout *Oncorhynchus mykiss*, and Caspian trout, but decreases pellet consumption in the Siberian sturgeon. The same diversity in taste responses to sodium chloride and calcium chloride was obtained using other methods for the assessment of taste preferences in fish. Some species, silver rockling *Gaidropsarus mediterraneus* and fugu *Fugu paradalis*, have negative or indifferent response to these two salts; rainbow trout, Nile tilapia *Oreochromis niloticus*, and zander *Stizostedion lucioperca* have positive responses (Andriyashev, 1944; Hidaka *et al.*, 1978; Adams *et al.*, 1978; Appelbaum, 1980).

Unlike salts and free amino acids, citric acid and sucrose are not contained in marine or fresh water of natural water bodies. It was found that citric acid is a highly efficient taste stimulus for all fish species studied, without respect to their response to salinity. For the roach, goldfish, and cichlasoma, as well as for the arctic flounder, citric acid has deterrent properties, whereas for the common wolffish, guppy, and nine-spined stickleback, attractive (Table 1). The high efficiency of citric acid as the taste stimulus was documented in many other fish species: in carp, tench, lake char, lake trout, arctic char *Salvelinus alpinus erythrinus*, and grayling *Thymallus thymallus* it causes a significant increase in pellet consumption, whereas in the grass carp, Siberian sturgeon, and the chum salmon *Oncorhynchus keta*, it reduces consumption (Kasumyan and Sidorov, 1992; Kasumyan *et al.*, 1993; Kasumyan and Kalzhaev, 1993; Kasumyan and Sidorov, 1995a, 1995b; Kasumyan and Morsi, 1996, 1997; Kasumyan, 1997; Kasumyan and Prokopova, 2001; Kasumyan and Sidorov, 2001). Citric acid has deterrent taste properties for the fugu (Hidaka *et al.*, 1978); silver rockling (Andriyashev, 1944); and juveniles of pike *Esox lucius*, zander, and of European cisco *Coregonus albula* (Appelbaum, 1980). But it is a taste stimulator for the Nile tilapia and *Tilapia zillii* (Adams *et al.*, 1988) and for juveniles of the eel *Anguilla anguilla* and of the rainbow trout (Appelbaum, 1980). Sucrose produced an indifferent taste response for the arctic flounder, common wolffish, cichlasoma, goldfish, and nine-spined stickleback, but was a stimulator for roach and guppy.

Thus, analysis of our and literature data did not reveal any relationship between the taste preference of the fish, whether marine or freshwater. This conclusion concerns both the substances which may have significant concentrations in natural waters (sodium chloride and calcium chloride) and the substances which are usually absent in nature (citric acid, sucrose). It is possible that a high concentration of sodium chloride in marine water could affect the reception of other taste stimuli by the fish. Electrophysiological data indicate that taste responses to some substances could be significantly suppressed or facilitated during constant baseline stimulation of taste receptors by other chemical substances (so-called cross-adaptation) (Caprio, 1988; Marui and Caprio, 1992). Indirect effects of substances constantly present in water on taste preferences in fish is an open question.

The fish species studied by us differ not only in their responses to salinity, but also in the feeding pattern and the composition and width of the food spectra. The species whose ration contains a significant amount of vegetation are especially interesting. Data on other groups of vertebrates indicated that herbivorous animals usually have positive responses to mono- and disacharides (Bronstein, 1950; Harborne, 1993) and other substances which are sweet to humans (Kassil, 1972).

Among the fish studied, the herbal component in the ration is most pronounced in the roach (Weatherley, 1987; Giles *et al.*, 1990; Horppila, 1994) and guppy (Dussault and Kramer, 1981). These were indeed the two species which showed a positive response to sucrose: the roach consumed two times more pellets with sucrose than control pellets; guppies, 9–22 times more (Kasumyan and Nikolaeva, 1997). The goldfish also consumes macrophytes (Borutskii, 1959; Kharitonova, 1963), but sucrose was an indifferent stimulus for this fish. In other species studied, herbal components are pronounced very weakly or are absent, and the fish do not respond to sucrose (Table 1). It is known from the literature that the dace and the grass carp, which consume vegetation (Verigin *et al.*, 1963; Bobrov, 1968; Stuge, 1973; Popov, 1975; Stuge, 1987), have a positive response to sucrose (Kasumyan and Morsi, 1997; Kasumyan, 1997). For such fishes as carp, chub, minnow *Phoxinus phoxinus*, char, lake trout, Siberian sturgeon, starred sturgeon, Caspian trout, and

the chum salmon, sucrose was an indifferent taste substance (Kasumyan and Sidorov, 1992; Kasumyan and Kazhlayev, 1993; Kasumyan and Sidorov, 1995b; Kasumyan and Morsi, 1996; Kasumyan, 1997). Only carp of the above listed fishes consumes vegetation, as in the goldfish studied in this work, but the proportion of herbal components in the fish ration is relatively small (Borutskii, 1950; Dmitrieva, 1957; Kharitonova, 1963; Lebedev and Spanovskaya, 1983). Other species are zoophagues and do not feed on vegetation or consume it rarely.

The relationship between a herbivorous feeding pattern and a positive response to the taste of sucrose is not always pronounced and in many cases is not confirmed. It was shown that food containing sucrose is preferred by eel, pike, zander, smelt, Nile tilapia, rainbow trout (Appelbaum, 1980; Jones, 1990), and silver rockling (Andriyashev, 1944), which are zoophagues and piscivorous predators. On the other hand, *Tilapia zillii*, a typical herbivorous fish, has an indifferent response to fractions extracted from lettuce leaves (*Lactuca sativa*), containing various monosacharides (Adams *et al.*, 1988).

The fish species studied by us also differ in the width of their food spectra. For example, the roach, according to the data of many investigators, is a euryphagous species (Zheltenkova, 1960; Grogorash *et al.*, 1973; Ermolin, 1977; etc.). The goldfish belongs to the same group of fish (Dmitrieva, 1957; Kharitonova, 1963). The arctic flounder is a bentivorous species with a broad feeding spectrum (Shubnikov *et al.*, 1970; Kalyakina and Tsvetkov, 1984; Ponomarev *et al.*, 2001), and the planktivorous species with a wide food spectrum include the guppy (Dessault and Kramer, 1981), nine-spined stickleback (Wootton, 1976; Maksimenko and Tokranov, 1994), and cichlasoma (Axelrod and Worderwinkler, 1993; Pausan, 1984). The common wolffish is characterized by a pronounced stenophagy (Barsukov, 1959; Karamushko and Shatunovskii, 1994).

Analysis of taste responses in the fish to classical taste substances indicates that the diversity of food organisms does not affect the number of attractive taste substances. For example, only one taste substance out of four had a clear stimulating effect on the arctic flounder, cichlasoma, and the nine-spined stickleback, which have broad feeding spectra, as well as on the stenophagous common wolffish. Two substances were stimulating for euryphagous roach and guppy, whereas not one was revealed for the euryphagous goldfish. The same results were obtained when we analyzed the response of fish to free amino acids. The roach and the goldfish responded positively to eight amino acids; the guppy, to five; and the arctic flounder, to none (Table 1). Thus, the number of attractive amino acids from 21 tested amino acids varies among the fish with wide feeding spectra from 38% (roach and goldfish) to none (arctic flounder). The results of other studies also indicate that there is no relation between the level of euryphagy and the number of attractive amino acids. For example, in the chum salmon, which is not euryphagous, 66% of amino acids were attractive, whereas in the carp with a wide feeding spectrum, only 23% were attractive (Kasumyan and Sidorov, 1992; Kasumyan and Morsi, 1996).

It is known, that free amino acids, which are included in food organisms of fish, may have not only attractive but also deterrent properties (Kasumyan, 1997). We could find such deterrent amino acids only in the food spectrum of the goldfish. Analysis of our own and literature data indicates that, as in the case of stimulus amino acids, there are no relationships between the level of euryphagy and the number of deterrent amino acids. Nonetheless, certain traits still point to the possibility of such a relationship, because in many species with a wide feeding spectrum, deterrent amino acids are usually absent or represented in insignificant amounts (roach, 0%; arctic flounder, 0%; goldfish, 9.5%, dace, 0%; minnow, 19%; and Siberian sturgeon, 5%) (Kasumyan, 1997).

Correlation analysis of taste preferences to classical taste substances revealed two cases of significant correlation (negative) out of 21 possible variants of a pairwise comparison of seven species. Data from the literature (in total, 22 species, including our own results) indicated that a significant correlation was found in 25 out of 253 comparisons, and this relationship was positive only in 12 cases. Similar results were obtained during correlation analysis of taste responses of fish to free amino acids, supporting a high level of species specificity of taste preferences in fish. In cases of positive correlation, the pairs of compared species usually include species very dissimilar with respect to lifestyle and systematics. Certainly, an increase in the number of studied species is necessary for more correct conclusions about these relationships. But it is clear that there is no direct link between the level of feeding specialization of the fish or their response to salinity and the diversity of attractive taste substances. The only exception is the species with a pronounced herbal component in feeding, which are characterized by a positive response to sucrose, whereas sucrose usually is an indifferent stimulus for zoophagous fishes. The absence of the relation between the taste preferences and the lifestyle of the fish, in our opinion, could be explained by species specificity of taste preferences, pronounced even in related species or in species with a similar ecology (Kasumyan, 1997; our data). Obviously, this uniqueness of the taste reception maintains the species specificity of the feeding spectra (Nikolsky, 1974).

Characteristics of the Behavioral Taste Response

The behavioral taste response in fish is relatively simple and includes several basic components: snap,

Table 2. The number of snaps of pellets with classical taste substances and free amino acids (L-stereoisomers) by the fish (S)

No.	Stimulus	Concentration, M	Roach		Goldfish		Guppy		Arctic flounder		Nine-spined stickleback		Common wolffish		Cichlasoma	
			S	*n*	S	*n*	S	*n*	S	*n*	S	*n*	S	*n*	S	*n*
	Classical taste substances															
1	citric acid	0.26	2.3 ± 0.3**	29	1.8 ± 0.2	64	1.6 ± 0.09**	101	1.5 ± 0.1	98	1.4±0.1***	76	1.7 ± 0.1	127	1.73	291
2	calcium chloride	0.9	2.0 ± 0.3	26	1.3 ± 0.1	60	1.3 ± 0.05	100	1.6 ± 0.1	98	3.0 ± 0.3	79	1.5 ± 0.1	123	1.38	272
3	sodium chloride	1.73	1.7 ± 0.2	26	1.1 ± 0.1	62	1.3 ± 0.06	101	1.7 ± 0.2*	98	2.3 ± 0.2	78	1.9 ± 0.1	120	1.77	279
4	sucrose	0.29	2.3 ± 0.4*	26	1.1 ± 0.1	65	1.4±0.07***	101	1.4 ± 0.1	98	2.9 ± 0.4	77	2.3±0.1***	141	1.47	268
	Free amino acids															
5	alanine	0.1	1.3 ± 0.1	35	1.2 ± 0.1*	40	2.4 ± 0.1***	101	1.1 ± 0.1	69	–		–		–	
6	arginine	0.1	1.2 ± 0.1	35	1.0 ± 0.1	41	1.9 ± 0.1*	100	1.0 ± 0.02*	70	–		–		–	
7	asparagine	0.1	1.6 ± 0.2	36	1.1 ± 0.1	42	2.2 ± 0.1***	100	1.3 ± 0.1	70	–		–		–	
8	asparagic acid	0.01	1.4 ± 0.1	37	1.1 ± 0.1	42	2.2 ± 0.1***	101	1.3 ± 0.1	70	–		–		–	
9	valine	0.1	1.6 ± 0.2	36	1.1 ± 0.1	42	2.1 ± 0.1***	100	1.3 ± 0.1	70	–		–		–	
10	histidine	0.1	1.8 ± 0.2	36	1.3 ± 0.1***	40	1.9 ± 0.1*	100	1.4 ± 0.1	70	–		–		–	
11	glycine	0.1	1.9 ± 0.3	31	1.1 ± 0.1	42	1.4 ± 0.1	101	1.1 ± 0.5	70	–		–		–	
12	glutamine	0.1	1.2 ± 0.1	36	1.5 ± 0.1***	42	2.2 ± 0.1***	100	1.2 ± 0.1	70	–		–		–	
13	glutamic acid	0.01	1.5 ± 0.2	36	1.0 ± 0.1	32	2.3 ± 0.1***	100	1.3 ± 0.1	70	–		–		–	
14	isoleucin	0.01	1.7 ± 0.2	36	1.0 ± 0.0	41	1.5 ± 0.1	100	1.1 ± 0.1	70	–		–		–	
15	leucin	0.01	1.3 ± 0.1	36	1.1 ± 0.1	39	2.3 ± 0.1***	100	1.0 ± 0.04	70	–		–		–	
16	lysine	0.1	2.2 ± 0.5	35	1.1 ± 0.1	34	1.7 ± 0.1	100	1.4 ± 0.1	70	–		–		–	
17	methionine	0.1	1.4 ± 0.1	34	1.2 ± 0.1*	40	2.7 ± 0.1***	100	1.2 ± 0.1	70	–		–		–	
18	norvaline	0.1	1.3 ± 0.1	37	1.2 ± 0.1	42	2.0 ± 0.1*	100	1.2 ± 0.1	70	–		–		–	
19	proline	0.1	2.2 ± 0.3*	38	1.6 ± 0.2**	37	2.4 ± 0.2***	100	1.3 ± 0.1	70	–		–		–	
20	serine	0.1	1.1 ± 0.1*	36	1.5 ± 0.2*	40	1.8 ± 0.1	100	1.0 ± 0.02*	70	–		–		–	
21	tyrosine	0.001	1.1 ± 0.1*	36	1.0 ± 0.1	44	2.5 ± 0.2***	100	1.3 ± 0.1	70	–		–		–	
22	threonine	0.1	1.2 ± 0.1	36	1.0 ± 0.0	44	1.9 ± 0.1*	101	1.2 ± 0.1	70	–		–		–	
23	tryptopfan	0.01	1.4 ± 0.1	35	1.4 ± 0.1***	40	3.8 ± 0.1***	100	1.1 ± 0.4	70	–		–		–	
24	phenylalanine	0.1	1.4 ± 0.2	35	1.1 ± 0.1	40	1.9 ± 0.1*	100	1.0 ± 0.02*	70	–		–		–	
25	cysteine	0.1	2.0 ± 0.4	35	1.1 ± 0.1	39	1.7 ± 0.1	101	1.0 ± 0.02*	70	–		–		–	
	Bloodworms extract															
26	series 1	75 g/l	1.1 ± 0.1	29	1.1 ± 0.1	67	1.2 ± 0.04	131	1.5 ± 0.1	98	1.2±0.1***	214	1.3±0.1***	144	1.21	207
27	series 2	75 g/l	1.0 ± 0.0*	43	1.0 ± 0.01	83	1.2 ± 0.1***	102	1.5 ± 0.1	98	–		–		–	
	Control															
28	series 1	–	1.4 ± 0.1	27	1.2 ± 0.1	59	1.3 ± 0.06	100	1.4 ± 0.1	98	2.8 ± 0.3	76	1.7 ± 0.1	117	1.4	244
29	series 2	–	1.5 ± 0.1	42	1.0 ± 0.0	40	1.6 ± 0.1	100	1.1 ± 0.1	70	–		–		–	

Note: See Note to Table 1.

Table 3. Duration of retention (retention time, Rt) of pellets with classical taste substances and free amino acids (L-stereoisomers) by the fish after the first snap

No.	Stimulus	Concentration, M	Roach		Goldfish		Guppy		Arctic flounder		Nine-spined stickleback		Common wolffish	
			Rt	*n*	Rt	*n*	Rt	*n*	Rt	*n*	Rt	*n*	Rt	*n*
	Classical taste substances													
1	citric acid	0.26	2.2 ± 0.9**	29	5.3 ± 0.7*	64	4.0 ± 0.3***	101	6.4 ± 0.4	98	1.4 ± 0.2**	76	1.2 ± 0.04***	127
2	calcium chloride	0.9	7.2 ± 1.5	26	7.4 ± 0.8	60	1.5 ± 0.2	100	6.0 ± 0.2	98	2.5 ± 0.3	79	1.3 ± 0.1**	123
3	sodium chloride	1.73	9.5 ± 1.7	26	5.7 ± 0.6*	62	1.1 ± 0.04***	101	6.8 ± 0.4	98	2.5 ± 0.3	78	1.4 ± 0.1*	120
4	sucrose	0.29	9.2 ± 1.7	26	7.4 ± 0.5	65	4.9 ± 0.3***	101	5.9 ± 0.3	98	3.6 ± 0.3	77	2.4 ± 0.1***	141
	Free amino acids													
5	alanine	0.1	9.1 ± 0.8**	35	9.4 ± 0.8	40	1.4 ± 0.1	101	4.2 ± 0.2	69	–		–	
6	arginine	0.1	9.2 ± 0.9**	35	10.3 ± 0.8*	41	1.2 ± 0.04*	100	4.4 ± 0.2	70	–		–	
7	asparagine	0.1	5.4 ± 0.7	36	7.5 ± 0.7	42	1.6 ± 0.1	100	3.6 ± 0.1	70	–		–	
8	asparagic acid	0.01	3.4 ± 0.7*	37	11.9 ± 1.0**	42	1.4 ± 0.1	101	5.1 ± 0.3***	70	–		–	
9	valine	0.1	6.9 ± 0.9	36	11.2 ± 0.7**	42	1.3 ± 0.1	100	4.3 ± 0.2	70	–		–	
10	histidine	0.1	5.9 ± 0.8	36	8.2 ± 0.9	40	1.4 ± 0.1	100	4.2 ± 0.1	70	–		–	
11	glycine	0.1	5.8 ± 0.7	31	10.7 ± 0.7**	42	9.5 ± 0.4***	101	4.2 ± 0.1	70	–		–	
12	glutamine	0.1	7.8 ± 0.8	36	6.7 ± 0.7	42	2.7 ± 0.1***	100	4.0 ± 0.2	70	–		–	
13	glutamic acid	0.01	5.1 ± 0.9	36	10.4 ± 1.4	32	5.2 ± 0.4***	100	4.6 ± 0.2*	70	–		–	
14	isoleucin	0.01	5.1 ± 0.9	36	12.4 ± 0.7***	41	1.2 ± 0.1*	100	4.2 ± 0.1	70	–		–	
15	leucin	0.01	6.9 ± 0.9	36	11.5 ± 0.6***	39	1.3 ± 0.1	100	5.0 ± 0.2***	70	–		–	
16	lysine	0.1	6.2 ± 1.0	35	7.2 ± 0.9	34	2.7 ± 0.3***	100	3.7 ± 0.2	70	–		–	
17	methionine	0.1	6.7 ± 0.8	34	6.4 ± 0.7	40	1.8 ± 0.1	100	4.7 ± 0.2**	70	–		–	
18	norvaline	0.1	8.8 ± 0.9*	37	7.2 ± 1.0	42	1.2 ± 0.04*	100	3.8 ± 0.2	70	–		–	
19	proline	0.1	6.4 ± 0.9	38	6.2 ± 0.8	37	1.5 ± 0.1	100	4.1 ± 0.2	70	–		–	
20	serine	0.1	9.2 ± 0.7**	36	8.8 ± 0.8	40	1.4 ± 0.1	100	4.0 ± 0.1	70	–		–	
21	tyrosine	0.001	8.2 ± 1.0	36	11.7 ± 0.7***	44	1.7 ± 0.1	100	4.4 ± 0.1	70	–		–	
22	threonine	0.1	10.0 ± 1.0***	36	9.7 ± 0.5*	44	1.3 ± 0.1	101	4.8 ± 0.4*	70	–		–	
23	tryptopfan	0.01	8.5 ± 1.0	35	5.9 ± 0.8	40	1.8 ± 0.1**	100	4.6 ± 0.2*	70	–		–	
24	phenylalanine	0.1	4.5 ± 0.7	35	6.6 ± 0.7	40	1.3 ± 0.1	100	3.5 ± 0.2	70	–		–	
25	cysteine	0.1	3.3 ± 0.8*	35	8.5 ± 1.2	39	2.7 ± 0.4***	101	4.4 ± 0.2	70	–		–	
	Bloodworms extract													
26	series 1	75 g/l	12.8 ± 1.2**	29	6.8 ± 0.2	67	7.1 ± 0.2***	131	5.2 ± 0.2*	98	3.8 ± 0.1***	214	2.3 ± 0.3*	144
27	series 2	75 g/l	10.5 ± 0.6***	43	9.7 ± 0.4*	83	9.6 ± 0.4***	102	5.2 ± 0.2***	98	–		–	
	Control													
28	series 1	–	7.1 ± 1.4	27	7.4 ± 0.5	59	1.7 ± 0.1	100	5.9 ± 0.3	98	3.0 ± 0.3	76	1.6 ± 0.1	117
29	series 2	–	5.9 ± 0.8	42	7.8 ± 0.8	40	1.5 ± 0.1	100	3.9 ± 0.2	70	–		–	

Note: See Note to Table 1.

Table 4. Duration of retention (retention time, RT) of pellets with classical taste substances and free amino acids (L-stereoisomers) by the fish throughout the entire test

No.	Stimulus	Concentration, M	Roach		Goldfish		Guppy		Arctic flounder		Nine-spined stickleback		Common wolffish		Cichlasoma	
			Rt	*n*	Rt	*n*	Rt	*n*	Rt	*n*	Rt	*n*	Rt	*n*	Rt	*n*
	Classical taste substances															
1	citric acid	0.26	4.1 ± 1.2*	29	6.4 ± 0.7	64	5.8 ± 0.4***	101	8.4 ± 0.8	98	4.9 ± 0.3	76	1.3 ± 0.1***	127	2.34	291
2	calcium chloride	0.9	14.9 ± 2.1*	26	8.1 ± 0.8	60	2.4 ± 0.2	100	7.9 ± 0.3	98	5.7 ± 0.7	79	1.4 ± 0.1	123	3.35***	272
3	sodium chloride	1.73	20.4 ± 2.3***	26	6.1 ± 0.6*	62	2.0 ± 0.2	101	9.6 ± 0.9	98	4.6 ± 0.6	78	1.5 ± 0.1*	120	1.4**	279
4	sucrose	0.29	19.2 ± 2.9**	26	7.7 ± 0.6	65	6.1 ± 0.3***	101	7.6 ± 0.5	98	6.4 ± 0.8	77	2.4 ± 0.2***	141	2.03	268
	Free amino acids															
5	alanine	0.1	11.1 ± 1.2**	35	9.6 ± 0.7	40	5.2 ± 0.5***	101	4.7 ± 0.4	69	–		–		–	
6	arginine	0.1	9.8 ± 0.8*	35	10.3 ± 0.8*	41	3.5 ± 0.3	100	4.5 ± 1.8	70	–		–		–	
7	asparagine	0.1	8.7 ± 1.5	36	8.0 ± 0.8	42	5.0 ± 0.3	100	4.9 ± 0.5	70	–		–		–	
8	asparagic acid	0.01	4.9 ± 1.0	37	12.0 ± 1.0**	42	4.1 ± 0.3**	101	6.0 ± 0.5*	70	–		–		–	
9	valine	0.1	8.0 ± 1.0	36	11.5 ± 0.6**	42	4.3 ± 0.4*	100	5.3 ± 0.4	70	–		–		–	
10	histidine	0.1	7.8 ± 0.8	36	9.1 ± 0.9	40	3.9 ± 0.3	100	5.6 ± 0.5*	70	–		–		–	
11	glycine	0.1	12.0 ± 1.9*	31	11.3 ± 0.7**	42	11.3 ± 0.3***	101	4.5 ± 0.2	70	–		–		–	
12	glutamine	0.1	8.1 ± 0.8	36	7.8 ± 0.8	42	8.5 ± 0.5***	100	5.1 ± 0.5	70	–		–		–	
13	glutamic acid	0.01	7.1 ± 1.6	36	10.8 ± 1.4*	32	10.3 ± 0.5***	100	5.3 ± 0.3	70	–		–		–	
14	isoleucin	0.01	6.8 ± 0.9	36	12.4 ± 0.7*	41	2.5 ± 0.2	100	4.6 ± 0.2	70	–		–		–	
15	leucin	0.01	8.0 ± 1.0	36	11.5 ± 0.6***	39	5.1 ± 0.5***	100	5.2 ± 0.2*	70	–		–		–	
16	lysine	0.1	10.6 ± 1.8	35	7.8 ± 0.8	34	4.8 ± 0.4***	100	4.6 ± 0.3	70	–		–		–	
17	methionine	0.1	7.9 ± 0.8	34	6.6 ± 0.7	40	6.2 ± 0.3***	100	5.1 ± 0.3	70	–		–		–	
18	norvaline	0.1	10.6 ± 0.9**	37	7.4 ± 0.9	42	3.8 ± 0.3	100	4.5 ± 0.4	70	–		–		–	
19	proline	0.1	10.5 ± 1.6	38	7.8 ± 0.8	37	5.3 ± 0.4***	100	4.4 ± 0.2	70	–		–		–	
20	serine	0.1	9.8 ± 0.8*	36	10.6 ± 1.7*	40	3.7 ± 0.4	100	4.2 ± 0.2	70	–		–		–	
21	tyrosine	0.001	8.7 ± 1.0	36	11.7 ± 0.7***	44	6.1 ± 0.5***	100	5.7 ± 0.5	70	–		–		–	
22	threonine	0.1	11.1 ± 1.1**	36	9.7 ± 0.5*	44	4.0 ± 0.3*	101	5.5 ± 0.5	70	–		–		–	
23	tryptopfan	0.01	10.1 ± 1.2*	35	6.9 ± 0.8	40	12.3 ± 0.6***	100	5.0 ± 0.2	70	–		–		–	
24	phenylalanine	0.1	5.2 ± 0.7	35	6.9 ± 0.7	40	3.5 ± 0.3	100	3.7 ± 0.2	70	–		–		–	
25	cysteine	0.1	6.3 ± 1.6	35	8.9 ± 1.2	39	4.9 ± 0.5***	101	4.5 ± 0.2	70	–		–		–	
	Bloodworms extract															
26	series 1	75 g/l	13.0 ± 1.1*	29	7.0 ± 0.2	67	7.8 ± 0.2***	131	6.0 ± 0.4**	98	42 ± 0.2**	214	2.4 ± 0.2***	144	3.07	207
27	series 2	75 g/l	10.5 ± 0.6**	43	9.7 ± 0.4*	83	11.1 ± 0.3***	102	6.0 ± 0.4*	98	–		–		–	
	Control															
28	series 1	–	8.5 ± 1.3	27	8.5 ± 0.9	59	2.5 ± 0.2	100	7.7 ± 0.4	98	5.5 ± 0.6	76	1.7 ± 0.1	117	1.97	244
29	series 2	–	7.2 ± 0.9	42	7.8 ± 0.8	40	3.0 ± 0.3	100	4.5 ± 0.3	70	–		–		–	

Note: See Note to Table 1.

Table 5. Spearman correlation coefficients among the behavioral taste responses of the fish to taste substances (classical taste substances and free amino acids collapsed)

Parameter of the behavioral taste response	Number of snaps			
	roach	goldfish	guppy	arctic flounder
Consumption of pellets, %	−0.53**	−0.54**	0.44*	0.16
Number of snaps				
Retention time after the first snap				

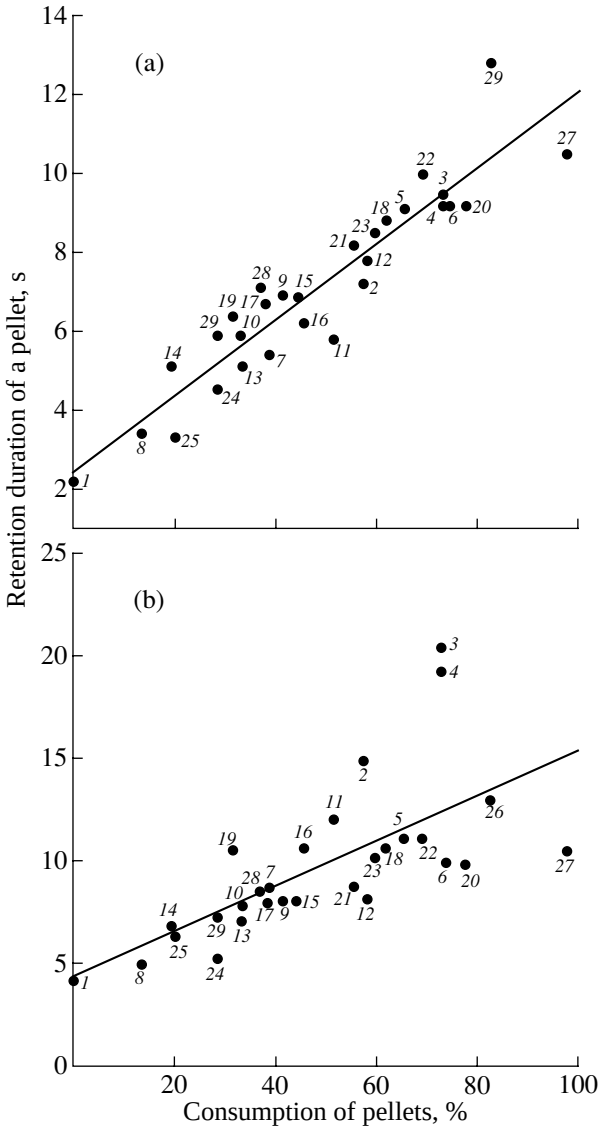
Parameter of the behavioral taste response	Retention time							
	after the first snap				throughout the entire experiment			
	roach	goldfish	guppy	arctic flounder	roach	goldfish	guppy	arctic flounder
Consumption of pellets, %	0.94***	0.66***	0.76***	0.11	0.80***	0.49**	0.48**	0.19
Number of snaps	−0.57**	−0.61**	−0.18	0.53**	−0.07	−0.41*	0.33	0.79***
Retention time after the first snap					0.76***	0.82***	0.75***	0.84***

Note: See Note to Table 1.

retention of the pellet in the oral cavity, rejection of the pellet, and its repeated snaps. The frequency and duration of these components differ and depend on the taste attractiveness of the pellet and the fish species (Table 2–4). The most variable is the retention time, which may differ in various fish species by a factor of 2–3. Responses of fish of the same species to pellets with an attractive or aversive taste differ in this measure even more.

Computation of the Spearman correlation coefficient between parameters of the taste response was conducted for the species which were tested with both classical taste substances and free amino acids. The well-pronounced positive relationship between taste attractiveness of the pellet and the duration of its retention was found in the goldfish. It is even more significant in the roach (Table 5, figure). Earlier (Kasumyan and Morsi, 1996), it was suggested that this relationship could be a characteristic trait of bentivorous fishes with the grazing strategy of feeding behavior. During feeding, such fishes consume a large amount of the bottom substrate and other incidental materials and use special mechanisms to separate food items (Sibbing *et al.*, 1986; Sibbing, 1991). Most probably, intraoral separation of food items requires additional time. Prolonged taste testing of a highly attractive food item may be characteristic of such fish as guppy (Kasumyan and Nikolaeva, 1997), which are planktivorous with a broad feeding spectrum (Dussault and Kramer, 1981). It may also be expected in the trout, juveniles of which predominantly feed on drift and large individuals become piscivorous predators (Ringler, 1979; L'abée-Lund *et al.*, 1992). Most probably, adequate and accurate identification of attractive substances and triggering the swallowing reflex requires a more prolonged time than rejection of unattractive food items. It is thought (Tamar, 1976; Kasumyan and Sidorov, 1993, 1994) that prolonged retention of the food item in the oral cavity allows more precise assessment of its taste properties. Quick rejection of unattractive food item minimizes unproductive expenses of time during feeding. However, these patterns are not universal, because in the chum salmon, the relationship between the duration of taste testing of the food item and its attractiveness is, unlike many other species, reverse (Kasumyan and Sidorov, 1992).

The average number of repeated snaps of the food item ranges from 1 to 1.5 and only rarely exceeds 2. Multiple rejections and repeated snaps of the pellet are less characteristic of river fishes, such as minnow, dace, chub, grayling, trout, etc. (Kasumyan and Sidorov, 1993; Kasumyan and Sidorov, 1995a; Kasumyan, 1997). This trait of the behavioral taste response may be an adaptation of the fishes to the current, where rejected food items could be soon transferred and become inaccessible. This also explains the small number of repeated snaps of the pellet by the arctic flounder, inhabiting the littoral of northern seas, where tidal currents are pronounced. In the fish living in stalled or slowly moving waters (carp and tench), the average number of repeated snaps is higher (Kasumyan and Morsi, 1996; Kasumyan and Prokopova, 2001). The number of repeated snaps in many fish correlated with the taste attractiveness of the pellet. In various species, this relationship could be opposite, negative in the roach, goldfish, and tench or positive in the guppy. In carp and trout, there is no significant correlation



Relationship between the duration of retention of pellets with classical taste substances and free amino acids (L-stereoisomers) and their taste attractiveness: (a) during the first snap of the pellet; (b) during the total experiment. The numbers agree with the number of substance in Tables 1–4.

between the number of repeated snaps and the taste attractiveness of the food item.

CONCLUSION

The basic chemosensory systems of fish, olfaction and taste, are involved in the behavioral response to artificial pellets containing chemical substances. Comparative analysis of behavioral responses of fish with excluded olfaction and intact fish using the methods applied in this work (Kasumyan and Morsi, 1996) showed that the absence of olfactory sensitivity does not cause any changes in the response to pellets with taste substances. The threshold concentrations to behavioral taste responses coincide in treated and intact fish. This suggests that the olfactory system is not involved in the behavioral response of fish to pellets with various substances and that the pattern and intensity of these responses are controlled solely by the taste system.

The results of the study indicate, that fish with different ecology have a well-developed taste system allowing to assess the properties of the food objects. The response of fish to taste stimuli is characterized by pronounced species specificity. This points to the important role of taste reception in feeding selectivity in fish. It is possible that we could not find any relation between the life mode and ecology of the species just because of this high species specificity of food spectra. The results of this study did not reveal any link between the environmental conditions (water salinity) or feeding pattern of the fish and its taste preferences.

Many patterns of taste reception in fish and specific characteristics of their response to various taste substances are very important in the applied aspect and could be used in fish culture and fisheries. Our studies showed that highly efficient stimulators and deterrent substances could be developed which may be used to manage the feeding behavior of fish. Our results can be used to increase the taste attractiveness of artificial fish foods, for correction of their content, by introduction of certain stimulant substances or rejection of deterrent substances. This would not only reduce direct losses of artificial foods in fish culture, but would facilitate more efficient conversion of food to fish growth because consumption of more attractive food is accompanied by more intense secretion of digestive enzymes (Takeda and Takii, 1992).

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