Taste Preferences and the Dynamics of Behavioral Taste Response in the Tench *Tinca tinca* (Cyprinidae)

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Abstract—Behavioral taste responses to four classic taste substances, 21 free amino acids (L-stereoisomers), and 19 organic acids were determined in the tench *Tinca tinca* using the behavioral methods of testing. Most substances (31 of 43) were food stimulators and increased consumption of agar pellets. The remaining 12 substances had individual taste properties. No deterrent substances were found. The comparison of taste preferences of the tench with eight other fish species, studied earlier, revealed a pronounced species specificity of the taste spectra. Threshold concentrations for the two most efficient taste substances, cysteine and maleic acid, were determined. Pellets with L-α-phenylalanine and L-β-phenylalanine had similar levels of consumption, whereas those with maleic and fumaric acids (cis- and trans-isomers of the phenylbutazonic acid) differed in consumption. Taste attractiveness of di- and tricarbonic acids was significantly higher than monocarbonic acids. With increasing length of the carbon chain, the stimulating effect of monocarbonic acids increased, whereas that of dicarbonic acids decreased. A negative relationship between the pH level of carbonic acid solution and the consumption level of the pellet was found. The basic characteristics of the dynamics of the behavioral taste response were analyzed using L-alanine (0.1 M) as the model substance. The retention time and between-shaps intervals were determined. It was found that the more shaps the fish exhibit during the test, the longer is the taste response. The length of the behavioral taste response was higher in tests terminated by consumption of the pellet. The retention time in these tests was longer than the intervals between shaps. The retention time reduced each successive bite, whereas the intervals between shaps changed less.

Taste reception is responsible for the determination of the quality of food items and the assessment of their properties to the food requirements of the organism. Taste buds, composing a peripheral area of the sensory system, have very similar structures in all fishes (Reutter, 1992; Jakubowski and Zuwala, 2000). Unlike other vertebrates, the taste system of fishes has several characteristic traits, involving the specificity of taste bud topography and their quantity. In many fish species of various systematic groups, taste receptors are located not only in the mouth cavity but also on the external surface of the body, on lips, barbels, head, body, caudal peduncle, and fins (Atems, 1971; Kapoor *et al.*, 1975; Gomahr *et al.*, 1992). Fishes differ from other groups of animals also by a greater number of taste receptors. Only the external taste buds reach several hundred thousand in some fishes (catfishes of the genus *Ictalurus*, see Atema, 1971; Finger *et al.*, 1991), which exceeds the total number of taste buds in birds and mammals, including humans, by a factor of ten (Kassil, 1972).

Characteristics of the distribution of taste buds caused the distinction between two specific chemosensory subsystems in fishes, oral (intraoral) and extraoral (Finger and Morita, 1985; Kanwal and Finger, 1992). Electrophysiological and behavioral experiments indicated that these two systems differ in sensitivity and the range and composition of stimuli detected (Marui and Caprio, 1992; Kasumyan, 1997), as well as in their role

in feeding behavior (Atema, 1980; Pavlov and Kasumyan, 1990, 1998). The structural development of the peripheral region of the taste system and the characteristics of taste bud topography are significantly associated with the life strategy and feeding pattern of the fish species. For fishes inhabiting upper water layers with good illumination and feeding during the daytime and for visual predators actively pursuing their prey, external taste buds are not numerous or are completely absent. In bentivorous fishes with a twilight or night peak of feeding, taste buds cover most or all of the external body surface (Kapoor *et al.*, 1975; Gomahr *et al.*, 1992). The latter fish also have a very high density of intraoral taste receptors, located on the jaws, palate, gill arches, on the pharynx, and at the beginning of the esophagus. For example, in bentivorous cyprinid fishes, the maximum density of intraoral taste buds reaches 300–600 per mm^2 or more (Sibbing *et al.*, 1986; Ossee *et al.*, 1997), which is 10–20 times more than in salmon (Hara *et al.*, 1993), which use vision to search for, detect, pursue, and catch their prey. In bentivorous fishes, the functions of intraoral taste receptors are associated not only with the assessment of the quality of food items but also with their separation from the bottom substrate taken by the fish during feeding (Sibbing *et al.*, 1986). This trait of bentivorous fishes attracted the attention of investigators to the study of their taste system, especially its morphological and functional characteristics.

Taste preferences in bentivorous cyprinid fishes have been most studied in the carp *Cyprinus carpio* (Kasumyan and Morsi, 1996). The aim of this study was the analysis of taste preferences in another representative of this family, tench *Tinca tinca*. According to morphological data, taste buds in the mouth cavity of the tench, as in the carp, are numerous and form zones with different densities of taste receptors (Zuwala and Jakubowski, 1993). A comparison of the taste preferences of these two species is especially interesting, because they are involved in interspecific competition and feed on similar food objects (Perkar and Krupauer, 1968; Sukop and Adamek, 1995). There is no data on the functional characteristics of the taste reception in the tench. The aims of this study included analysis of the taste responses of the tench to various taste substances (classic taste substances, free amino acids, and organic acids predominantly of the carboxylic array), determination of the threshold concentrations for some of these substances, and analysis of the dynamics of the behavioral taste response in the tench.

MATERIALS AND METHODS

Early juveniles of the tench at the age of 1.5 months were obtained from the Russian Federal Institute of Pond Fisheries (VNIIPRKh, Moscow oblast), and were reared for two years on live foods (first zooplankton, mostly Cladocera, and then on bloodworms, Chironomidae larvae). Experiments were conducted on 15 two-years-olds (1998) and 13 three-years-olds (1999) of the tench, which had an average body length (TL) of 7.8 and 8.6 cm, and on average weight of 4.8 g and 6.4 g, respectively. Several days before the experiments, the fish were transferred individually in plastic aquariums with a volume of about 4.5 l. The front wall of the observational aquarium was transparent; the other walls were opaque. The aquariums were covered with special covers with a hole in the center to provide food or agar pellets. AN-4 air pumps were used for aeration. The average water temperature during the experiments was 22–25°C. Partial water exchange in the aquariums was done every week. During the experimental period, the fish were fed bloodworms once per day after testing.

Immediately after transfer to the test aquariums, the fish were trained to take the food introduced into the aquarium; first it was separate chironomid larvae, and then agar pellets containing a water extract of chironomid larvae (175 g/l). The pellets were introduced into the aquarium individually, with an interval of 10–15 min. After several days of training, the fish positioned themselves under the hole in the aquarium cover and took the pellets in 100% of cases. The bite on the pellet occurred either immediately after it appeared in the water or after 2–3 s.

After training, we began the experiments, in which we recorded the behavioral taste response to the introduced pellet containing one of the tested substances or an extract of bloodworms. In control experiments, we used pellets that did not contain any food substances. In each experiment that started after introduction of the pellet, we recorded the following parameters: (1) the number of shaps of the pellet up to the moment of final consumption or rejection, (2) retention time (s) of the pellet after the first bite and during the whole test, and (3) final ingestion of the pellet, i.e., whether it was ingested or rejected. The moment of the pellet consumption was determined by the termination of characteristic chewing movements of the fish jaws and the restoration of normal movements of gill covers. The retention time was recorded with an Agat hand stop watch. The tests in which there was no bite by the fish within one minute after introduction were excluded from the analysis. The pellets with various taste substances and pellets with bloodworm extract and control pellets were introduced in a random sequence. Rejected or not taken pellets were removed from the aquarium immediately after termination of the test.

In a separate series of experiments on the dynamics of the behavioral taste response, we recorded the duration of successive periods of retention of the pellet by the fish and the periods between shaps. A special computer program BH-Fish was developed for this purpose, which allowed us to record the time interval with a precision of 0.1 s. Recording of these events (sequence of shaps and rejections during a single test) involved pressing certain keys or mouse buttons on a personal computer.

All pellets, including control pellets, were bright red. We used the dye Ponceau (5 μm), which was introduced into the agar gel during the pellet preparation. The pellets (length 4.0 mm, diameter 1.35 mm, volume 5.72 mm^2) were prepared using a stainless steel tube immediately before the experiment. A more detailed description of the preparation and storage of the gel is given elsewhere (see Kasumyan and Sidorov, 1994b; Kasumyan and Morsi, 1996). All substances used as taste stimuli (four classic taste substances, 21 free amino acids, 19 organic acids) represented preparations with a high degree of chemical purity. The list of the substances and their concentrations is given in Tables 1, 2, and 5.

In total, 8500 experiments on taste preferences for various substances and 110 experiments on the dynamics of the behavioral taste response were conducted. Experiments with classic taste substances and free amino acids were conducted in three-year-old tenches, whereas the tests with organic acids and various concentrations of cysteine and maleic acid were performed on three-year-old fish. Experiments on the dynamics of the behavioral taste response were also conducted on three-year-old fish. We recorded the proportion of ingested pellets and the following index of food preference (or food attractiveness):

$$\text{Ind}_{pal} = \frac{R - C}{R + C} \times 100,$$

where R is the percentage of the ingested pellets with the substance and C is the percentage of control pellets (Kasumyan and Morsi, 1996). The statistical analysis of the data involved χ^2 and the Student's t-tests and the Spearman rank correlation coefficient (r_s).

RESULTS

Classic taste substances. Three of the four classic taste substances had a stimulation effect for the tench, causing significant increases in the proportion of the ingested pellets (Table 1). The citric acid had the maximum attractiveness; its attractiveness was similar to the attractiveness of chironomid larvae. The consumption of pellets with calcium chloride or sodium chloride was significantly lower than pellets with citric acid, but two times higher than consumption of control pellets. Sucrose did not affect the consumption of pellets. In most cases, the responses of the fish to attractive pellets also significantly differed from the responses of the fish to control pellets in all other measures, the number of shaps, and retention time during the first bite and the whole all duration of the test. The longest retention time was characteristic of pellets with chironomid extract and citric acid. Consumption or rejection of these pellets occurred, as a rule, after the first bite.

Free amino acids. We did not find substances with deterrent properties for the tench among amino acids and classic taste substances. Most amino acids (12 out of 21) caused a significant increase in the consumption of pellets (Table 2). The strongest attractive taste for the trench was noted for cysteine; its presence in the pellet composition brought about almost 100% consumption. Other stimulating amino acids were much less efficient. The average retention time of pellets with various amino acids considerably varied (from 2–3 s to 23 s) and significantly correlated with their attractiveness

(Table 3). Variability of the average number of shaps of pellets in experiments with amino acids was lower (from 1.0 to 2.1), and there was no significant correlation between this measure and other measures of the behavioral taste response. Pellets with highly attractive cysteine were ingested by the fish mostly after the first bite (in 144 out of 146 tests in which the pellets were ingested). Retention of pellets with this substance by the fish was 3–5 times longer than with other amino acids (Table 2). Pellets with less attractive or indifferent amino acids were characterized by significantly shorter retention time by the fish, and repeated rejections and shaps of the pellet during the test occurred much more frequently. For example, in certain experiments, pellets with serine, arginine, asparatic acid, glutamic acid, and tyrosine were taken by the fish up to 7–8 times. Comparison of the consumption of pellets with α-phenylalanine and β-phenylalanine did not reveal any significant differences ($p > 0.05$).

Due to the high stimulation effect of cysteine, we conducted special experiments to determine the threshold concentration of this amino acid. It was found that with a decrease in its concentration, the attractiveness of pellets with cysteine significantly reduces, as did most other measures of the behavioral taste response. At the concentration 0.01 M, the attractive properties of cysteine disappeared, and at 0.0001 M there were no significant differences between cysteine and control pellets in other measures of the behavioral taste response (for the number of shaps and retention time, see Table 4).

Organic acids. Most organic acids (17 out of 19) had an attractive taste for the tench. The stimulating action of seven amino acids—maleic, α-ketoglutaric, oxalic acid, tartaric, malic acid, citric acid, and malonic acid—was highest (the level of consumption of the pellets was 70%). Pellets with these amino acids were

Table 1. Taste responses of tench to classic taste substances

Stimulus	Concentration, M (%)	Consumption of pellets, %	Index of taste attractiveness, %	Number of shaps	Retention time, s		Number of tests
					after the first bite	during the whole experiment	
Extract of chironomids	175.0	98.7 ± 0.9***	59.2	1.1 ± 0.0***	18.4 ± 0.5***	19.1 ± 0.4***	150
Citric acid	0.26(5.0)	90.7 ± 2.3***	56.4	1.1 ± 0.0***	26.4 ± 0.9***	26.9 ± 0.9***	150
Sodium chloride	1.73(10.0)	54.7 ± 4.0***	36.8	1.5 ± 0.1***	11.7 ± 0.7***	13.2 ± 0.6**	150
Calcium chloride	0.9(10.0)	50.7 ± 4.1***	33.4	1.4 ± 0.1***	10.3 ± 0.7***	12.1 ± 0.7	150
Sucrose	0.29(10.0)	31.3 ± 3.8	10.6	1.9 ± 0.1***	8.2 ± 0.6	10.5 ± 0.6	150
Control	–	25.3 ± 3.6	0	2.5 ± 0.2	6.9 ± 0.5	10.8 ± 0.6	150

Note: Concentration of chironomid larvae is given in g/l. Significance of differences from the control:
    * $p < 0.05$;
    ** $p < 0.01$;
    *** $p < 0.001$.

Table 2. Taste responses of tench to free amino acids (L-stereoisomers)

Stimulus	Concentration, M (%)	Consumption of pellets, %	Index of taste attractiveness, %	Number of shaps	Retention time, s		Number of tests
					after the first bite	during the whole experiment	
Cysteine	0.1	97.3 ± 1.3***	87.1	1.0 ± 0.0***	23.0 ± 0.6***	23.2 ± 0.6***	150
Alanine	0.1	57.7 ± 4.1***	79.2	1.6 ± 0.1**	8.1 ± 0.5***	10.4 ± 0.5***	142
Proline	0.1	46.0 ± 4.5***	74.6	1.7 ± 0.1	6.7 ± 0.4***	8.6 ± 0.5***	124
Serine	0.1	35.9 ± 4.0***	68.5	1.9 ± 0.1	5.8 ± 0.4***	7.8 ± 0.5***	142
Arginine	0.1	24.5 ± 7.6***	57.1	1.6 ± 0.1**	4.4 ± 0.2***	6.1 ± 0.3***	144
Lysine	0.1	24.1 ± 3.6***	56.5	1.6 ± 0.1***	4.3 ± 0.2***	6.1 ± 0.4**	145
Metyonine	0.1	22.5 ± 3.8***	54.1	2.0 ± 0.1	3.2 ± 0.2**	6.1 ± 0.4**	120
Glutamine	0.1	19.9 ± 3.3**	49.6	1.9 ± 0.1	4.3 ± 0.5***	6.3 ± 0.5**	146
Glycine	0.1	16.9 ± 3.1*	43.2	1.6 ± 0.1**	3.6 ± 0.2***	4.9 ± 0.3	148
Asparagine	0.1	15.0 ± 3.0*	38.2	1.7 ± 0.1*	3.7 ± 0.3***	5.4 ± 0.3	140
Valine	0.1	14.9 ± 3.0*	38.0	1.6 ± 0.1**	3.2 ± 0.2*	4.6 ± 0.3	141
Gystidine	0.1	14.1 ± 2.9	35.6	1.6 ± 0.1**	3.2 ± 0.2**	4.6 ± 0.3	142
Norvaline	0.1	10.6 ± 2.6	22.5	1.6 ± 0.1**	2.9 ± 0.2	4.3 ± 0.3	142
Treonine	0.1	9.5 ± 2.4	17.3	1.5 ± 0.1	3.1 ± 0.3	4.5 ± 0.4	148
α-phenylalanine	0.1	7.1 ± 2.4	2.9	1.5 ± 0.1***	2.1 ± 0.2	2.9 ± 0.2***	113
β-phenylalanine	0.1	6.8 ± 2.4	0.7	2.3 ± 0.1	2.4 ± 0.1	5.0 ± 0.3	103
Aspartic acid	0.01	17.7 ± 3.4**	45.1	2.1 ± 0.1	3.9 ± 0.4***	6.3 ± 0.5**	124
Glutamine acid	0.01	11.5 ± 2.9	26.4	2.0 ± 0.1	3.5 ± 0.3**	5.4 ± 0.4	122
Leycine	0.01	6.7 ± 2.3	0	1.9 ± 0.1	2.6 ± 0.2	4.3 ± 0.3	120
Isoleycine	0.01	6.5 ± 2.2	–1.5	1.8 ± 0.1	2.5 ± 0.2	4.1 ± 0.4	123
Triptophane	0.01	3.4 ± 1.5	–32.7	2.0 ± 0.1	2.6 ± 0.2	4.3 ± 0.3	148
Tyrosine	0.001	6.3 ± 2.0	–3.1	1.9 ± 0.1	2.7 ± 0.2	4.5 ± 0.3	143
Control	–	6.7 ± 2.3	–	2.0 ± 0.1	2.5 ± 0.2	4.6 ± 0.3	120

Note: see note to Table 1.

Table 3. Spearman correlation coefficients between measures of the behavioral taste response of the tench to taste substances

Measures of the response	Number of shaps	Retention time	
		after the first bite	during the whole experiment
Consumption of pellets, %	–0.27/–0.89***/–0.71***	0.94***/0.96***/0.96***	0.92***/0.96***/0.94***
Number of shaps	–	–0.19/–0.85***/–0.66***	–0.03/–0.77***/–0.54***
Retention time	–	–	0.94***/0.95***/0.96***

Note: *, **, and *** as in Table 1. Taste responses to free amino acids are given before the first slash; to organic acids, between the two slashes; and total to free amino acids, organic acids and classic taste substances, after the second slash.

ingested mostly after the first bite and a long retention in the mouth cavity. Only two amino acids, acetic and cholic, did not greatly affect the consumption of pellets by the fish. On the whole, for all organic acids we found a good relationship between the consumption of pellets, on the one hand, and the number of shaps and the retention time, on the other hand (Table 5).

Experiments for determining the level of taste sensitivity of the tench to various organic acids were conducted with maelic acid, which was one of the most efficient acids. It was found that the stimulating action of maleic acid is expressed within the range of concentrations from 0.1 to 0.01 M. After reduction of the concentration to 0.001 M, the effect disappears. Decrease

Table 4. Taste responses of tench to various concentrations of L-cysteine and malic acid

Stimulus	Concentration, M (%)	Consumption of pellets, %	Index of taste attractiveness, %	Number of shaps	Retention time, s		Number of tests
					after the first bite	during the whole experiment	
Cysteine	0.1	90.1 ± 3.1***	91.5	1.2 ± 0.1***	18.6 ± 1.0***	19.7 ± 1.0***	91
Cysteine	0.05	61.5 ± 5.1***	87.8	1.5 ± 0.1	12.8 ± 0.8***	14.8 ± 0.8***	91
Cysteine	0.025	37.8 ± 5.1***	80.9	1.5 ± 0.1	6.3 ± 0.5***	7.3 ± 0.6***	90
Cysteine	0.01	7.8 ± 2.5	32.2	1.6 ± 0.1	3.1 ± 0.3*	4.1 ± 0.4*	115
Cysteine	0.001	7.9 ± 3.1	32.8	1.6 ± 0.1	2.3 ± 0.3	3.2 ± 0.4	76
Control	–	4.0 ± 2.3	0	1.5 ± 0.1	2.1 ± 0.2	2.9 ± 0.3	75
Malic acid	0.1	90.7 ± 2.4***	95.3	1.1 ± 0.0***	19.8 ± 0.6***	20.2 ± 0.6***	150
Malic acid	0.05	53.3 ± 4.1***	92.1	1.3 ± 0.1***	13.3 ± 0.8***	14.9 ± 0.8***	150
Malic acid	0.01	14.7 ± 2.5***	74.0	1.3 ± 0.0***	5.3 ± 0.5***	6.1 ± 0.7**	204
Malic acid	0.001	3.7 ± 2.6	27.1	1.4 ± 0.1**	2.2 ± 0.3	3.3 ± 0.5	54
Control	–	2.2 ± 0.0	0	2.6 ± 0.2	2.3 ± 0.2	4.1 ± 0.3	225

Note: see Table 1.

Table 5. Taste responses of tench to organic acids

Stimulus	Concentration, M (%)	Consumption of pellets, %	Index of taste attractiveness, %	Number of shaps	Retention time, s		Number of tests
					after the first bite	during the whole experiment	
Maleic acid	0.1	90.6 ± 2.3***	97.2	1.0 ± 0.0***	19.8 ± 0.6***	20.2 ± 0.6***	150
α-ketoglutaric acid	0.1	90.6 ± 2.3***	97.2	1.0 ± 0.0***	18.6 ± 0.5***	18.7 ± 0.5***	150
Oxalic acid	0.1	89.3 ± 2.5***	97.1	1.1 ± 0.0***	15.7 ± 0.6***	16.2 ± 0.5***	150
Tartaric acid	0.1	83.3 ± 3.0***	96.9	1.1 ± 0.0***	17.3 ± 0.7***	18.5 ± 0.7***	150
Malic acid	0.1	78.0 ± 3.3***	96.7	1.1 ± 0.0***	16.6 ± 0.7***	17.0 ± 0.6***	150
Citric acid	0.1	76.0 ± 3.4***	96.6	1.1 ± 0.0***	27.0 ± 5.3***	16.0 ± 0.7***	150
Malonic acid	0.1	72.6 ± 3.6***	96.5	1.2 ± 0.1***	14.3 ± 0.8***	16.0 ± 0.8***	150
Glycolic acid	0.1	55.3 ± 4.0***	95.4	1.4 ± 0.1***	13.5 ± 0.8***	14.7 ± 0.7***	150
Succinic acid	0.1	29.3 ± 3.7***	91.5	1.5 ± 0.1***	6.7 ± 0.5***	7.4 ± 0.5***	150
Fumaric acid	0.1	24.6 ± 3.5***	90.0	1.8 ± 0.1***	7.0 ± 0.6***	8.7 ± 0.7***	150
Capronic acid	0.1	22.6 ± 3.4***	87.9	1.3 ± 0.1***	6.0 ± 0.6***	6.7 ± 0.6**	150
Adipinic acid	0.1	21.3 ± 3.3***	88.5	2.8 ± 0.3	5.3 ± 0.6***	8.3 ± 0.6***	150
Valeric acid	0.1	16.0 ± 3.0***	85.0	1.9 ± 0.1***	4.3 ± 0.5***	6.2 ± 0.6*	150
Butyric acid	0.1	16.0 ± 3.0***	85.0	1.6 ± 0.1***	4.2 ± 0.5***	5.2 ± 0.5	150
Ascorbic acid	0.1	11.3 ± 2.5***	79.4	3.6 ± 0.2	4.7 ± 0.3***	7.8 ± 0.4***	150
Formic acid	0.1	7.3 ± 2.1*	69.8	2.1 ± 0.1**	3.0 ± 0.3***	4.8 ± 0.4	150
Propionic acid	0.1	7.3 ± 2.1*	69.8	1.7 ± 0.1***	3.5 ± 0.4*	4.6 ± 0.5	150
Acetic acid	0.1	5.3 ± 1.8	60.6	1.7 ± 0.1***	2.6 ± 0.3	3.5 ± 0.4*	150
Cholic acid	0.1	1.3 ± 0.1	0	2.9 ± 0.3	2.2 ± 0.2	4.4 ± 0.4	150
Control	–	1.3 ± 0.9	0	3.1 ± 0.3	2.3 ± 0.2	4.7 ± 0.4	150

Note: see Table 1.

Table 6. Duration of consecutive retentions of pellets with L-alanine (0.1 M) by the tench, and intervals between shaps in tests terminated by ingestion or rejection of the pellet

Number of shaps in the test	Number of tests	Duration of consecutive phases of the test, s											Duration of the test, s
		R_1	I_{1-2}	R_2	I_{2-3}	R_3	I_{3-4}	R_4	I_{4-5}	R_5	I_{5-6}	R_6	
Tests, terminated by ingestion of the pellet													
1	28	8.1 ± 1.5	–	–	–	–	–	–	–	–	–	–	8.1 ± 1.5
2	14	7.8 ± 1.1	6.3 ± 1.3	4.7 ± 0.9	–	–	–	–	–	–	–	–	21.7 ± 2.1
3	6	7.4 ± 1.8	2.3 ± 0.6	5.2 ± 1.2	6.6 ± 2.5	2.4 ± 0.6	–	–	–	–	–	–	23.4 ± 2.2
4	2	8.7 ± 0.0	2.0 ± 1.3	4.4 ± 2.5	3.8 ± 0.5	2.3 ± 0.8	10.0 ± 3.3	1.0 ± 0.3	–	–	–	–	34.5 ± 1.1
5	2	2.4 ± 0.9	0.7 ± 0.4	8.2 ± 6.4	6.2 ± 5.3	2.6 ± 1.2	1.3 ± 1.0	3.4 ± 1.2	10.4 ± 1.1	5.2 ± 2.0	–	–	40.5 ± 2.0
6	2	4.2 ± 2.1	3.5 ± 2.0	1.6 ± 0.9	2.2 ± 1.9	3.1 ± 1.7	2.5 ± 2.2	2.2 ± 1.4	3.4 ± 2.7	1.7 ± 0.5	6.7 ± 1.1	2.3 ± 0.4	33.1 ± 0.5
Average	–	7.6 ± 0.8	4.5 ± 0.9	4.8 ± 0.7	5.6 ± 1.6	2.5 ± 0.4	5.4 ± 2.1	2.2 ± 0.7	6.9 ± 2.3	3.5 ± 1.3	6.7 ± 1.1	2.3 ± 0.4	
Tests, terminated by rejection of the pellet													
1	21	2.5 ± 0.5	–	–	–	–	–	–	–	–	–	–	2.5 ± 0.5
2	20	2.1 ± 0.5	7.7 ± 2.6	1.6 ± 0.3	–	–	–	–	–	–	–	–	15.2 ± 2.9
3	8	1.9 ± 0.5	9.5 ± 6.3	1.3 ± 0.1	4.6 ± 2.0	1.0 ± 0.2	–	–	–	–	–	–	18.3 ± 6.0
4	5	2.4 ± 0.8	1.7 ± 1.2	1.3 ± 0.2	2.1 ± 0.9	1.4 ± 0.3	1.1 ± 0.5	1.4 ± 0.2	–	–	–	–	11.4 ± 1.3
5	2	1.2 ± 0.2	0.3 ± 0.1	1.0 ± 0.2	2.1 ± 1.4	4.2 ± 3.1	1.4 ± 0.9	0.6 ± 0.3	2.6 ± 1.3	1.0 ± 0.5	–	–	15.0 ± 1.8
Average	–	2.2 ± 0.3	6.8 ± 2.1	1.5 ± 0.2	3.4 ± 1.1	1.5 ± 0.4	1.1 ± 0.4	1.2 ± 0.2	2.6 ± 1.3	1.0 ± 0.5	–	–	
All tests													
1	49	5.7 ± 0.9	–	–	–	–	–	–	–	–	–	–	5.7 ± 0.9
2	34	4.4 ± 0.7	7.1 ± 1.5	2.9 ± 0.5	–	–	–	–	–	–	–	–	17.6 ± 1.9
3	14	4.2 ± 1.1	6.4 ± 3.6	3.0 ± 0.7	5.7 ± 1.6	1.6 ± 0.3	–	–	–	–	–	–	20.4 ± 3.5
4	7	4.2 ± 1.3	1.8 ± 0.9	2.2 ± 0.8	2.6 ± 0.7	1.6 ± 0.3	4.4 ± 2.0	1.3 ± 0.2	–	–	–	–	18.0 ± 4.4
5	4	1.8 ± 0.5	0.5 ± 0.2	4.6 ± 3.3	4.1 ± 2.5	3.4 ± 1.4	1.3 ± 0.5	2.0 ± 1.0	6.5 ± 2.4	3.1 ± 1.5	–	–	27.7 ± 7.4
6	2	4.2 ± 2.1	3.5 ± 2.0	1.6 ± 0.9	2.2 ± 1.9	3.1 ± 1.7	2.5 ± 2.2	2.2 ± 1.4	3.4 ± 2.7	1.7 ± 0.5	6.7 ± 1.1	2.3 ± 0.4	33.1 ± 0.5
Average	–	4.7 ± 0.5	5.8 ± 1.2	2.9 ± 0.4	4.6 ± 1.0	2.0 ± 0.3	3.3 ± 1.2	1.6 ± 0.3	5.5 ± 1.8	2.6 ± 1.0	6.7 ± 1.1	2.3 ± 0.4	

Note: Retention (R_1, R_2, R_3, etc.) of pellet after the first, second, third, etc. shaps. Intervals between the first and the second (I_{1-2}), second and third (I_{2-3}), third and fourth (I_{3-4}), etc. shaps of the pellet.
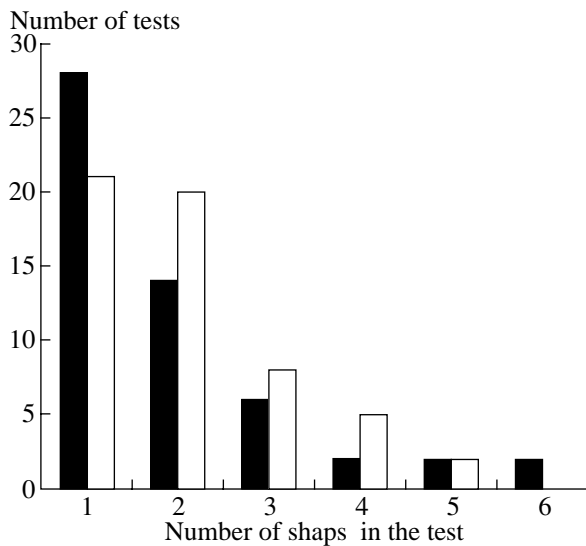
Number of tests

Fig. 1. Experiments with various number of shaps of pellets, containing L-alanine, 0.1 M, by the tench. Dark bars represent experiments, terminated by ingestion; open bars, by rejection of the pellet.
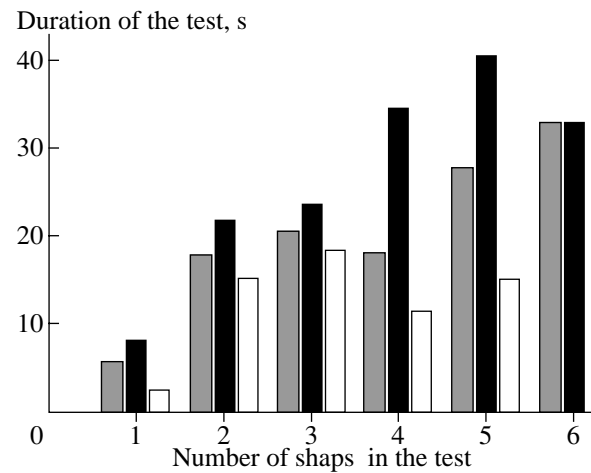
Duration of the test, s

Fig. 2. Relationship between the average duration of the behavioral taste response of the tench and the number of shaps of the pellets with L-alanine, 0.1 M. Dark bars represent experiments, terminated by ingestion, open bars, by rejection of the pellet, gray bars represent all experiments.

of the concentration consistently caused a reduction of the retention time and an increase of the number of shaps in the experiment (Table 4).

Dynamics of the behavioral taste response. Pellets with alanine were used to determine the dynamics of the behavioral taste response in the fish. We chose this amino acid, because a relatively large average number of repeated shaps (1.6, Table 2) was observed in experiments with alanine. It was also important that before final ingestion or rejection of the pellet the fish retained it in the mouth cavity for a prolonged time. The choice of alanine was also associated with almost 50% consumption of pellets, allowing us to conduct separate analysis of tests terminated with ingestion or rejection of the pellet. These methodic traits made the experiments easier. Two out of 15 individuals characterized by individual response measures close to the average values were chosen for this experiment.

The consumption of pellets with alanine in this series of experiments was 54%; the average duration of the test was 12.4 s. In most cases, we observed 1–2 shaps of the pellet; the maximum number of shaps was 6 (Fig. 1). The duration of the experiment was directly related to the number of repeated shaps of the pellet (Fig. 2) and ranged from 5.7 s in the case of one bite to 33.1 s for six shaps (Table 6). On average, the retention time was significantly shorter (2.72 s) than the intervals between the shaps (4.52 s). The longest retention time was observed after the first bite; the longest interval was found between the first and the second shaps (Table 6). After subsequent shaps, there was a tendency to reduce the retention time and intervals between shaps (Fig. 3).

Similar results were obtained in separate analyses of the dynamics of behavioral taste response in tests terminated by either ingestion or rejection of the pellet. The retention time was longer after the first bite than after subsequent shaps and decreased with each subsequent bite. The intervals between the subsequent shaps were reduced in experiments with rejection but remained at approximately the same level in experiments with ingestion of the pellet. The duration of the taste response was significantly longer in experiments in which the pellet was ingested by the fish (Table 6, Figs. 2 and 3).

DISCUSSION

With respect to the life strategy and relative development of sense organs, tench should be considered as a microsmatic fish species, because chemoreception plays an important role in its behavior. Nonetheless, chemosensory systems of this fish, their morphology, and functional characteristics still remain poorly studied. Most of the existing studies were devoted to the olfactory system, especially its structural organization (Teichmann, 1954; Wunder, 1957; Doving et al., 1977), function (Adrian and Ludwig, 1938; Devitsina and Malyukina, 1977; Dubois-Dauphin et al., 1980), and the behavioral responses of this fish to some olfactory stimuli (Schultz, 1956). The data on the taste system of the tench are limited to the distribution and cytology of taste buds (Zuwala and Jakubowski, 1993) and their dysfunction caused by the action of heavy metals (Haider, 1975). It has been found that, with respect to the structure, extra- and intraoral taste buds in the tench are similar in morphology. Their density in the mouth cavity ranges from 63 per mm^2 on the glossohyale to 170 per mm^2 in the distal part of the throat adjacent to the esophagus. The density of taste buds on the lips of
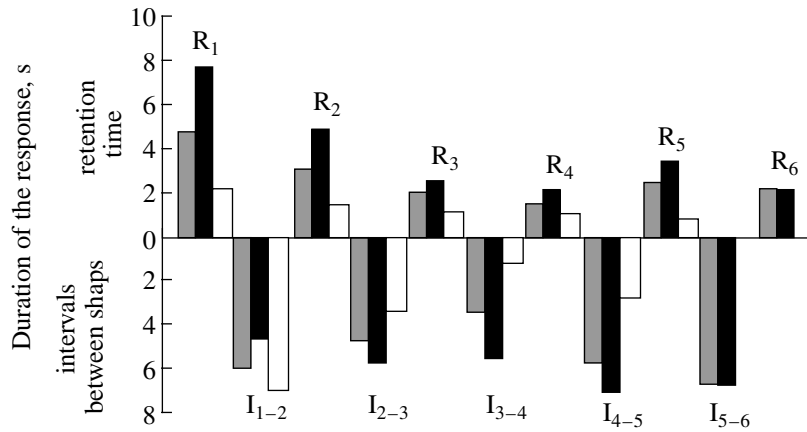
Fig. 3. Duration of consecutive periods of the behavioral taste response of the tench to pellets with L-alanine, 0.1 M. R_1, R_2, R_3, etc. denote, respectively, the first, second, third, etc. periods of retention; I_{1-2}, I_{2-3}, I_{3-4}, etc. denote, respectively, the intervals between the first and the second, second and third, and third and fourth shaps of the pellet. For other symbols, see Fig. 2.

the fish is, on average, 66 per mm² at the external surface of the head, and from 20 in the interorbital area to 12 per mm² in the occipital area (Zuwala and Jakubowski, 1993).

The results of our study indicate that the tench can detect the presence of various substances in the pellet and behaviorally differentiate most of them. Most of the substances used in this study were food stimulators for this fish: inclusion of some of these substances into the agar pellet caused a significant increase of the consumption of this pellet. The remaining 12 substances had indifferent taste properties. No deterrent substances were found, which distinguish trench from other studied fish species that have both stimulating or indifferent substances and also deterrent ones (Kasumyan, 1997). The behavioral taste responses of the tench are characterized by a significant consistency: the consumption of pellets with citric acid, cysteine, and alanine was high in various series of experiments conducted within a one-year interval. Other measures of the behavioral taste response were also very similar, which emphasizes the stability of the behavioral taste response of the fish to highly attractive substances.

In our opinion, these characteristics of the taste sensitivity of the tench—the broad range of stimulating taste substances and the absence of deterrent stimuli—is one of the mechanisms of high-feeding flexibility in this fish species, allowing it to switch between various food objects easily. According to the data from the literature, plankton organisms (Cladocera, Copepoda) dominate as the food of younger age groups of the tench (Frankiewicz et al., 1991). Older individuals feed on various representatives of macrozoobenthos (larvae of chironomids and other insects, mollusks, and oligochaetes; see Weatherley, 1959; Kennedy and Fitzmaurice, 1970; O'Maoileidigh and Bracken, 1989; Giles et al., 1990; Lammens and Hoogenboezem,

1991). After a worsening of the food resources of the water body or an increase of food competition with other fish species, tench switch to other food: animalcules (Bryozoa) and their statoblasts, ostracodes, Heteroptera, detritus, and even to macrophytes and aerial insects that have fallen on the water surface, i.e., all available objects (Sukop and Adamek, 1995).

Data on taste preferences of fish obtained with the same method and concerning the responses of the fish to the same taste substances in the same concentrations remain very limited. Nonetheless, these data can be used for comparative analysis. The Spearman's correlation coefficients for consumption of pellets with amino acids and classic taste substances between nine fish species, including the tench, indicated that, in most cases, there are no correlations between the compared species (Table 7). This completely supports the earlier hypothesis that taste preferences completely differ between different fish species (Kasumyan, 1997; Kasumyan and Nikolaeva, 1997). This also agrees with most electrophysiological studies of the taste system in fishes (Ishida and Hidaka, 1987; Marui and Caprio, 1992; Hara et al., 1999). Significant relationships were found only in 6 out of 36 possible paired comparisons of taste preferences of free amino acids in various fish species, and 10 out of 36 for free amino acids and classic taste substances. Detailed analysis revealed that even the significant correlations were small and borderline in significance ($p < 0.05$) in four out of six cases. However, in the comparison of fish responses to free amino acids and classic taste substances, six out of ten such relationships had high-significance levels ($p < 0.01$ and $p < 0.001$). This suggests that taste preferences of the fish to various amino acids, representing adequate taste stimuli and contained in various food objects, are characterized by higher species specificity than taste preferences to the classic taste substances used in this study.

Table 7. Spearman rank correlation coefficient of taste preferences of free amino acids and classic taste substances between different fish species

Species	Carp, *Cyprinus carpio* (Kasumyan and Morsi, 1996)	Arctic charr *Salvelinus alpinus erythrinus* (Kasumyan and Sidorov, 1995)	Caspian trout *Salmo trutta caspius* (Kasumyan and Sidorov, 1993, 1994b)	Chum salmon *Oncorhynchus keta* (Kasumyan and Sidorov, 1992)	Russian sturgeon *Acipenser gueldenstaedtii* (Kasumyan, 1999)	Siberian sturgeon *A. baerii* (Kasumyan and Kozhlayev, 1993; Kasumyan, 1999)	Starred sturgeon *A. stellatus* (Kasumyan and Kozhlayev, 1993; Kasumyan, 1999)	Guppy *Poecilia reticulata* (Kasumyan and Nikolaeva, 1997)
Tench	0.33/0.57**	−0.004/0.24	−0.04/0.21	−0.29/−0.43*	0.08/–	−0.36/−0.62**	0.22/−0.15	0.23/0.28
Carp	–	0.45*/0.60**	0.40/0.53**	−0.22/−0.37	0.03/–	−0.30/−0.57**	0.15/−0.23	0.48*/0.49*
Arctic charr		–	0.64**/0.70***	0.01/−0.31	0.31/–	0.15/−0.16	0.03/−0.20	0.07/0.19
Caspian trout			–	−0.23/−0.49*	0.47*/–	−0.10/−0.36	0.15/−0.17	−0.03/0.07
Chum salmon				–	−0.63**/–	−0.25/0.25	−0.03/0.26	−0.45*/−0.44*
Russian sturgeon					–	0.30/–	0.14/–	0.26/–
Siberian sturgeon						–	−0.10/0.36	−0.004/−0.17
Starred sturgeon							–	−0.13/−0.25

Note: For tench, Carp, Arctic charr, Caspian trout, Chum salmon, and starred sturgeon, the correlations involve taste responses to 21 free amino acids and 4 classical taste substances; for the Siberian sturgeon, taste responses to 19 free amino acids (without cysteine and norvaline) and 4 classic taste substances; for Russian sturgeon, to 21 free amino acids. The correlation coefficient for free amino acids is presented before the slash; correlations for free amino acids and classical taste substances, after the slash. *, **, and ***, see Table 1.

The comparison between the carp and the tench—two related fish species characterized by a similar life mode and often inhabiting the same bodies of water and feeding on the same food—is especially interesting. In cases of common living and good availability of food resources, the food spectra of these two species may completely coincide (Perkar and Krupauer, 1968). A worsening in the feeding conditions causes strong food competition between carp and tench, and the latter usually cannot sustain competition with more active carp (Sukop and Adamek, 1953), which can penetrate deeper in the bottom substrate in search for food (Suetov, 1939). Comparison of amino acid food spectra revealed that in the tench, which is a more flexible and euryphagous species, the number of stimulating amino acids (120 is two times higher than in the carp (6). Deterrent amino acids were not found in the tench, but a small number of them were found in the carp (Kasumyan and Morsi, 1996). In spite of the coincidence of the consumed food organisms under good feeding conditions and the taxonomic relatedness of these fish species, there was no significant correlation between the amino acid taste spectra in carp and tench (Table 7). Similar results were obtained earlier after a comparison of three related species of sturgeons (genus

Acipenser): starred, Russian, and Siberian sturgeons (Kasumyan and Sidorov, 1994a; Kasumyan, 1999).

Comparison of taste preferences in carp and tench, however, revealed some degree of similarity. For example, for both carp and tench the most attractive amino acid was cysteine, which exceeded all other free amino acids in its level of attractiveness and was close to the attractiveness of chironomid larvae. Proline, asparatic acid, alanine, and glutamine were also attractive amino acids for both carp and tench. Only one amino acid, glutamine, was an indifferent taste stimulus for the tench but efficient in the carp. Thus, five out of six free amino acids, releasing significant increase of pellet consumption in carp, had the same effect on the tench. Moreover, the same amino acid (out of 21 tested) was the most efficient stimulus in both compared species. The responses of carp and tench to classic taste substances was also similar: the highest and equal attractiveness levels were characteristic of citric acid (the index of food preference in tench was equal to 56.4; in carp, 53.9). The responses of both of these fish species to sodium chloride and sucrose also coincided (Kasumyan and Morsi, 1996). Comparative analysis demonstrated that there is a certain similarity of taste preferences in fish with related taxonomy and similar

life strategy, at least for some taste stimuli. Certainly, additional studies are necessary before it becomes clear as to what is the relationship between systematic position and taste preferences in fishes.

The threshold concentrations of the two most efficient taste substances for the tench, cysteine and maleic acid, is equal to 2.5×10^{-2} and 10^{-2} M, which is very close or even coincides with the same values found in the carp (Kasumyan and Morsi, 1996), Caspian trout *Salmo trutta caspicus* (Kasumyan and Sidorov, 1994b), Siberian sturgeon (Kasumyan and Kozhlayev, 1993), and fugu *Fugu pardalis* (Hidaka, 1982), but is lower than in the Kamchatka steelhead *Oncorhynchus mykiss*, 10^{-4} (Jones, 1989). However, it should be noted that experiments with the Kamchatka steelhead were conducted using a method that differed with respect to taste substance presentation and behavior response recording. Calculations indicated that, at the threshold concentration of the taste substance, one pellet contains 17.3 μg of cysteine and 6.6 μg of maleic acid. The really active quantity of the taste substance causing a significant increase in the pellet consumption is lower, because only a small surface part of the substance interacts with the taste system of the fish. It should also be noted that the value of the threshold concentration does not necessarily coincide when various measures of the behavioral taste response are used as the criterion. The values of the threshold concentrations, as well as the responses of the fish, to all taste substances used in this study most probably reflect the functioning of the intraoral taste reception system. Earlier experiments using similar methods indicated that anosmic fish do not differ in the pattern or intensity of the behavioral taste responses and have the same level of sensitivity (Kasumyan and Morsi, 1996). Similar results were obtained in experiments comparing behavioral taste responses in intact and anosmic juveniles of the Atlantic salmon *Salmo salar* (Sutterlin and Sutterlin, 1970).

It is known that fishes exhibit a very high olfactory sensitivity to bile acids and their salts (Doving *et al.*, 1980; Selest and Doving, 1980; Hellstrom and Doving, 1986). For some of these fishes, these substances are efficient taste stimuli. For example, in electrophysiological experiments the threshold concentration of the sodium salt of taurolithoholic acid was 10^{-12} M, which is several orders lower than for many free amino acids (Hara *et al.*, 1999). However, cholic acid was an indifferent stimulus for the tench and did not affect the level of pellet consumption, the number of shaps, and the retention time. The absence of electric responses in the taste nerves after stimulation of taste buds by salts of bile acids has been documented in the carp, catfish *Plotosus lineatus*, and Nile tilapia *Tilapia nilotica* (Marui and Caprio, 1992).

In studies devoted to taste reception in fishes, significant attention is paid to the search for structural or physico-chemical characteristics, which could account for, or correlate with, the taste properties of a particular

substance. Electrophysiological data indicate that fishes can respond differently to stereoisomers and structural isomers of amino acids with different locations for the functional groups in the molecule. In the catfish *I. punctatus*, the amino acid L-α-alanine caused more intense electric responses in the nerve fibers from the taste buds located at the maxillar barbels of these fish than L-β-alanine (Caprio, 1978). In our experiments, the level of consumption of pellets with L-α-phenylalanine and L-β-phenylalanine coincided ($p < 0.05$) (Table 2). No statistically significant differences in the retention time of the pellet after the first bite were found ($p < 0.05$). However, two other measures of the behavioral taste response, the number of shaps and the retention time during the whole test (the differences between the taste response to L-α-phenylalanine and L-β-phenylalanine), were highly significant ($p < 0.001$). These results do not provide any unanimous conclusion about the ability of the fish to distinguish between these taste substances, whose structured modifications differed only slightly.

Nonetheless, changes in the configuration and structural alterations of the molecule of carbonic acids are significantly reflected in their taste attractiveness. For example, the efficiency of maleic and fumaric acids, representing cis- and trans-isomers of phenylbutazonic acid, differ significantly ($p < 0.001$). The same differences were found between acids with the same number of carbon atoms and carboxylic groups, but which differed by an additional double bond or additional functional groups. For example, an additional double bond in the molecule brings about a significant increase in the taste attractiveness of maleic acid as compared with its analogous acid, in which the double bond is absent (succinic acid). The addition of hydroxyl groups, one in the molecule of glycocholic acid in comparison to acetic acid, and two in the molecule of tartaric acid as compared to succinic acid, causes the same effect.

In the catfish *I. punctatus*, it was found that the most efficient taste stimuli are free amino acids with molecules devoid of electric charge and which contain three–four carbon atoms (Caprio, 1978). The relationship between the stimulating efficiency in alifatic and aromatic acids of the carboxyl array and the size of the molecule has been documented in electrophysiological experiments conducted on the carp (Marui and Caprio, 1992). In the tench, there was no significant correlation between the molecular weight of the substance and its taste attractiveness in the case of free amino acids ($r_s = 0.38$, $p = 0.09$), but it was significant in the case of carbonic acids ($r_s = 0.72$, $p < 0.01$). Our data point to certain relations between the taste attractiveness of carbonic acids and structural characteristics of their molecules such as the number of carbon atoms and carboxyl groups. These relations are inverse. For example, with an increase in the length of the carbon chain, the stimulating action of monocarbonic acids tends to increase, but it decreases in saturated dicarbonic acids (Fig. 4). The same relationship was found between the number
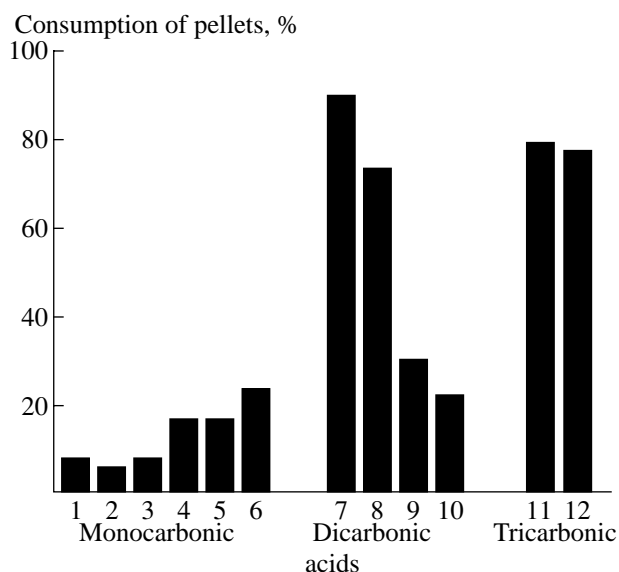
Consumption of pellets, %

Fig. 4. Taste attractiveness of mono-, di-, and tricarbonic acids (0.1 M) with various number of atoms of carbon in the molecule. Formic (1, C-1), acetic (2, C-2), propionic (3, C-3), butyric (4, C-4), valeric (5, C-5), capronic (6, C-6), oxalic (7, C-2), maleic (8, C-3), succinic (9, C-4), adipinic (10, C-10), malic (11, C-4), and citric (12, C-6) acids.

of carbon atoms in the molecule of alifatic monocarbonic acids and the intensity of behavioral and electrophysiological responses in juveniles of the Atlantic salmon (Sutterlin and Sutterlin, 1970). A rapid growth of taste attractiveness is clear in saturated acids with four carbon atoms in the molecule (Fig. 4). Comparative analysis of the efficiency of mono-, di-, and tricarbonic acids also agrees with this pattern. Our results indicate that the taste attractiveness of seven monocarbonic acids, except for glycolic acid, was low or completely absent (acetic acid), whereas all nine dicarbonic acids caused a significant increase in the pellet consumption. Five of the latter were highly efficient, with the consumption level over 70%. Both tricarbonic acids—malic and citric acids—also were highly efficient taste stimuli. Di- and tricarbonic acids are ranked first in the taste attractiveness array, whereas monocarbonic acids are last (Table 5).

Literature data on the relationship between the intensity of taste preferences in fish and the pH of the stimulus solution are contradictory. In experiments with the rainbow trout, in which more than 80 concentrations of free amino acid solutions were tested, this relationship was not found, even though the pH level ranged from 3.06 to 10.87 (Jones, 1989). However, the relationship between the consumption of agar gel and the pH of the solution introduced into the gel was clear in the tilapia, *T. zillii*. The lower the pH of the stimulus solution, the greater the amount of gel which was ingested by the fish. The relationship was nonlinear, and two carbonic acids (malic acid and citric acid) and three free amino acids (lysine, glutamine and asparatic

acids) at 0.01 M concentration were used as the taste substances (Adams *et al.*, 1988). In the tench, the relationship between the consumption of the pellets and the pH level of the solution of organic acids of the carboxyl array was also significant ($r_s = -0.84$; $p < 0.001$, Fig. 5). Taking account of the high species specificity of taste preferences in fish, determined in the case of free amino acids and classic taste substances, it is likely that the response of fish of various species to the taste of organic acids also differs significantly. Therefore, the relationship between the pH of the solution and its attractiveness for other fish species may be different. It is known that the behavioral taste responses to organic acids depend not only on the presence of hydrogen (H^+) ions in water but also the acid residual (R–COO) formed as a result of dissociation (Beidler, 1967; Ganzevles and Kroeze, 1987a, 1987b; Frank *et al.*, 1992). The role and significance of each of these components in the behavioral taste response still remains unclear.

As it has already been noted, ingestion or final rejection of the pellet usually occurs after several rejections and repeated shaps of the pellet. The average number of repeated shaps in tests with different taste substances usually exceeds 1.0 and reaches 3.6 (ascorbic acid) (Tables 1, 2, and 5). Up to eight–ten repeated shaps were observed in some tests. Our data on the dynamics of the behavioral taste responses of the fish to the pellet indicate that more repeated shaps correlated with longer taste response (Fig. 2). This concerns the tests terminated by ingestion of the pellet and the tests in which it was finally rejected. The duration of the behavioral taste response in the latter case was significantly shorter, first because of shorter retention time. The retention time of the pellet rapidly decreased for each repeated bite, whereas the intervals between them change less significantly. Thus, the time spent by the fish for assessment of the taste of the food item consecutively decreases with each repeated bite. It is possible that the dynamics of the behavioral taste response studied in the tench may be different in other fish species.

The values of one-time retention of the pellet by the fish are especially interesting. This time is required for a whole complex of processes: reception of the taste substance, transmission of the information to the taste centers, its analysis, development of the appropriate behavioral response, ingestion of the pellet or its rejection for subsequent bite, or final rejection. In experiments with alanine, the average values of one-time retention varied from 1.0 to 8.7 s, in cases of ingestion of the pellet, to 0.6–4.2 s, in cases of its rejection. In humans, the duration of the behavioral taste response (the time from the administration of the taste substance to the taste receptors to the time of response) to above-threshold concentrations of taste substances varied from 0.4 to 0.8 s, depending on the type and concentration of the substance (Yamamoto and Kawamura, 1981). Most of this time, which in fish varies more widely than in humans, is required for information
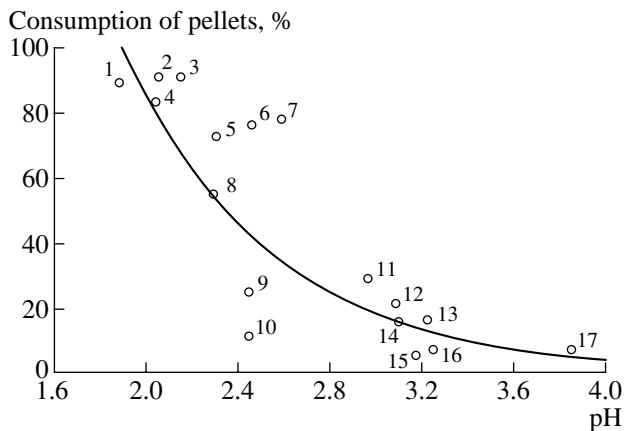
Consumption of pellets, %

Fig. 5. Relationship between the taste attractiveness of organic acids and the pH of their stimulus solution (0.1 M). Acids: oxalic (1), maleic (2), α-ketoglutaric (3), tartaric (4), malonic (5), citric (6), malic (7), glycolic (8), fumaric (9), ascorbic (10), succinic (11), adipinic (12), butyric (13), valeric (14), acetic (15), propionic (16), and formic (17).

analysis in brain centers and development of the appropriate behavioral response (Halpern, 1986).

The duration of behavioral taste response in fish depends on many factors. As in humans, one such factor in the tench is the concentration of the substance. Increasing the concentration increases the retention time and therefore the duration of the behavioral taste response (Table 4). In humans, however, this relationship is inverse: an increase in the concentration of the active substance reduces the duration of the taste response (Halpern, 1986). The taste quality of the stimulus and the lifestyle of the fish species significantly affect the duration of the behavioral taste response of the fish. For example, a strong positive relationship between the retention time and the attractiveness of the stimulus substance was found in bentivorous and some other fishes, e.g., carp and guppy (Table 3) (Jones, 1989; Kasumyan and Morsi, 1996; Kasumyan and Nikolaeva, 1997). In the tench, this relation was also well expressed. In rheophilic fishes feeding on detritus (e.g., Caspian trout), this relationship is weaker or is reverse (chum salmon) (Kasumyan and Sidorov, 1992, 1994b). For example, in experiments with a standard set of free amino acids as the taste substances, the retention time after the first bite varied in the Caspian trout and chum salmon from 0.9–3.5 and 0.1–3.3 s, respectively; and in carp, tench, and guppy from 1.5–16.5, 2.1–23.0, and 1.2–9.6 s, respectively (Table 2) (Kasumyan and Morsi, 1996; Kasumyan and Nikolaeva, 1997). It is suggested that fish living in a current are characterized by a rapid behavioral taste response due to a lower number of repeated shaps of the food object, because they retain a high efficiency of feeding when the prey can be removed by the stream (Kasumyan, 1997). A significant reduction of all measures of the behavioral

taste response is caused by pollution (heavy metals, low pH) (Kasumyan and Morsi, 1998).

Tench is a traditional species of pond culture in many European countries, and it was recently introduced in Australia, New Zealand, North America, Southeastern Asia, and Africa. In some places of its species range, tench is a game fish. Therefore, data on taste preferences of this fish may hold practical significance for the development of technologies for its rearing and feeding, as well as for the development of artificial lures. Data on the dynamics of the behavioral taste response of the tench is important for further understanding of the final phase of complex feeding behavior.

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