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by I. V. Burkovski1

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Department of the Zoology of Invertebrates, Moscow State University.

Zoologicheskiy zhurnal //Zoological Journal/,1970, volume 33, Norwege, 29, 497-507. <u>Ecology of the White Sea Tintinnida (Ciliata).</u> By I.V. Burkovskiy tment of the Zoology of Invertebrates, Moscow State University. ADUCTION NON For fauna; ten of these are important species. The average density of infusorians in summer in the 0-25 meter layer is 43 thousand specimens per cubic meter, and the biomass is 3.8 milligrams per cubic meter (collected by net). The majority of the species develop in the 0-10 meter layer; the density of infusorian occurrence decreases with depth. The maximum depth of infusorian penetration is 100 meters. During the course of a year changes of dominant species are observed in relation to changes in temperature. The majority of species attain their highest abundance in the summer. The density of tintinnids in winter is 10 to 100 specimens per cubic meter. The distribution of infusorians over the water area is spotty. It is affected by temperature, food, competition and certain other factors.

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In the past decade interest has markedly increased towards the tintinnids, one of the most extensively occurring groups in marine plankton. Data have appeared on the abundance (Margalef, 1963;Zeitschel, 1966; Pertsova and Chibisova, 1970 and others), feeding and reproduction of these infusorians (Gold, 1969, 1970, 1973; Pavlovskaya, 1971; Spittler, 1973 and others). In combination with the accumulating data on the consumption and assimilability of infusorians by various invertebrates and fish larvae (Epshtein, 1957; Margalef, 1963: Pavlovskaya and Pechen', 1971 and others), they permit us to understand the important role of the tintinnids in plankton associations. It is true that only a very few items have so far been studied and we are discussing here a very general concept. More specific studies of this concept depend on future, in particular ecological, studies in the field at the species and population levels.

Material was collected in the White Sea from 1970 to 1973. As fishing gear we used a plankton net No. 77 mesh silk bolting cloth with an entrance diameter of 19 centimeters. A total of 132 quantitative samples were processed. Vertical distribution was studied using data from 7 stations located in Kandalaksha Bay (2 stations) and in the White Sea Basin. The samples were taken in July 1971 and 1972 from the 0-5, 5-10, 10-15, 15-20, 20-25, 25-50, 50-100 and in one instance, 100-200 meter levels. Seasonal distributions were studied using data from 6 stations located in Kandalaksha Bay. During 1971-1972 samples were taken 3 times per month from June to September and once a month from October to May. The distribution of infusorians in the White Sea, the deep-water regions of Kandalaksha and Dvina Bays, and partly Gorlo and Onega Bay (the location of the stations is shown in figs. 6 and 9). Samples were taken July 29-31, 1972 from the 0-25 meters level. The plankton was fixed with a 4% solution of neutral formalin. The infusorians were counted under a

microscope. Identification was conducted according to available reports (for more details see the article of Burkovskiy et al., 1974).

To evaluate inter-species relations we used a mathematical analysis of niches (Lane and Naught, 1970). This method permits us to determine the interaction of species on the basis of their distribution, by means of the equation:

$$a_{ij} = \frac{\Sigma_h P_{ih} P_{jh}}{\Sigma_h P_{ij}},$$

where  $a_{ij}$  is the effect of the species j upon the species i  $(a_{ji}$  is the opposite effect),  $P_{i(j)}$  is the ratio of the idividuals of species i(j) in a medium h to the abundance of species i(j) in the entire medium, and h is the local medium (actual sample). The value  $1/\Sigma_h P$  ih<sup>2</sup> determins the width of the species niche.

The effect of species i upon species j is usually not identical to the inverse effect; therefore the two factors  $(a_{ij} \text{ and } a_{ji})$  are calculated simultaneously. When a = 0 there is no interaction; when a = 1 the interspecies interaction is equal to the intraspecific interaction, i.e., each individual of another species is considered to be [identical with] the individual of one's own species. Interaction of all the species may be graphically represented (fig. 7). Poor interaction between the species is a consequence of their sharing of the biotype (where  $a_{ij}$  and  $a_{ji}$  are less than 0.5), and strong interaction (where  $a_{ij}$  and  $a_{ji}$  are greater than 0.5) infers a distribution of the food resources between them.

E.A. Zamyshlyak and N.P. Poskryakova have been of great assistance to me in the collection and initial processing of the material. Data on phytoplankton and nannoplankton gathered by associates of the Department of Hydrobiology, Moscow University, have been used in this paper. I express my sincere gratitude to all of them. /498

Species and size composition. The White Sea fauna contains 20 species of tintinnids (Burkovskiy and others, 1974). Ten of these attain great abundance, and the remaining ones occur very rarely. Out of several taxonomically closely related species, as a rule, only one develops successfully. The genus Tintinnopsis is an exception, five of its six species being numer-The sizes of tintinnids vary within a very wide range. The smallest ous. of them, Tintinnopsis nana, hardly reaches 20 microns in length, while the largest, Parafavella denticulata, exceeds 400 microns. Other species form a continuous series within this range. The differences in size enable the tintinnids to use the biotope to the fullest possible extent. Fig. 1 combines data on the size and occurrence of the infusorians. We clearly see that out of 2 or 3 species which are similar in size usually only one will be success-The order in which abundant and rare species alternate cannot be explained ful. only by the fact that the conditions favour the development of some and inhibit that of others. Here competition probably plays a certain role. Undoubtedly, similar size makes possible a similar ecology, and the closer the taxonomical position of the species the greather this similarity. Here the genus Tintinnopsis is representative. The species of this genus form a significant size series almost without overlapping. Where sizes do coincide, only one species develops (T. beroidea and T. tubulosa).

Occurrence, density and biomass. Table 1 presents quantitative data on 10 abundantly occurring species. The small-sized species have the highest density. The average total density of the tintinnids in the 0 - 25 meter layer is approximately 43 thousand individuals per cubic meter (more than 1 million individuals per square meter), and the average total biomass is 3.8 milligrams per cubic meter (approximately 95 milligrams per square meter). These indices are rather high and fully comparable with those that we got previously for psammophilous infusorians (on the littoral: from 1 to 7 million

"Translator's note. Appeared in original text as "biotype".

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Figure 1. Size composition of the tintinnids.

1 - <u>Tintinnopsis nana</u>, 2 - <u>Steenstrupiella robusta</u>, 3 - <u>Tintinnopsis parvula</u>, 4 - <u>Leprotintinnus bottnicus</u>, 5 - <u>Codonellopsis pusilla</u>; 6 - <u>Helicostozella</u> <u>subulata</u>, 7 - <u>Stenosemella oliva</u>, 8 - <u>Codonellopsis ovata</u>, 9 - <u>Salpingella</u> <u>acuminata</u>, 10 - <u>Codonellopsis lata</u>, 11 - <u>Tintinnopsis beroidea</u>, 12 - <u>T. tubulosa</u>, 13 - <u>Ptychocylis obtusa</u>, 14 - <u>P. arctica</u>, 15 - <u>Parafavella</u> (?) <u>obtusa</u>, 16 -<u>Tintinnopsis fimbriata</u>, 17 - <u>T. campanula</u>, 18 - <u>Coxliella meunieri</u>, 19 -<u>Favella taraikaensis</u>, 20 - <u>Parafavella denticulata</u>; black boxes signify abundant species, white ones, rare species.

Key to Figure 1.

1 - Species; 2 - Volume of individuals, thousands per cubic micron.

individuals per square meter and from 100 to 300 milligrams per square meter) (Burkovskiy, 1971). If we take into consideration that the plankton net catches only a portion of the infusorians (according to our calculations only  $\frac{1}{4}$  of them<sup>\</sup>, and that the early stages of the development of the tintinnids, which are shell-less, as well as other plankton infusorians, which do not build any loricae, have completely escaped our field of view, then the figures we have presented should be increased by at least one order. The tintinnids are irregularly distributed in the White Sea (fig. 9) forming in some regions

dense accumulations, where their bioceonotic role must be very considerable. This applies particularly to littoral regions (up to three miles), where the biomass reaches 40 milligrams per cubic meter.

Habitat. The chief habitat factors of marine tintinnids include food, temperature, competition, predators and salinity.

## Table 1.

Quantitative description of the tintinnids (average data on the White Sea in the 0-25 meter layer, July 1972).

	· ·	$\mathbf{c}$	ч Удельный вес, %		0	
y. Baast	Плотность, тыс. экз/м <sup>3</sup>	Бномасса, <i>мг/м</i> ³	5 ПО ЧИСЛЕН- НОСТИ	с по био- массе	NOCTL.	
Helicostomella subulata Codonellopsis ovata Tintinn opis mana Parafavella denticulata Tintinnepsis beroidea T. companula Phychocylis obtusa Faveila taraikaensis Tintinnopsis parvula T. fimbriata	23,2 7,7 3,9 2,2 2,0 1,9 0,8 0,6 0,6 0,3	0,79 0,53 0,01 1,00 0,21 0,74 0,15 0,24 0,01 0,09	53,5 17,8 9,0 5,7 4,4 1,5 1,4 1,3 0,6	21,3 13,8 0,1 26,4 5,5 19,4 4,0 5,7 0,1 2,4	100 95 18 100 90 75 70 76 33 11	
Все виды вместе	43,0	3,80	100,0	100,0	-	

Key to above table:

1 - Species;

2 - Density, in thousands of individuals per cubic meter;

3 - Biomass, in milligrams per cubic meter;

4 - Relative significance, in %:

5 - by abundance;

6 - by biomass;

7 - Occurrence in %;

8 - All species together.

The tintinnids can catch and devour a wide range of organisms. Food. In their digestive vacuolae (particularly distinct in live preparations) we find bacteria, flagellates, peridinians and diatoms. The literature includes data on the feeding of infusorians on organic substances dissolved in sea water (Gold, 1969). According to our data, small infusorians predominantly feed upon bacteria, and larger infusorians, additionally on various algae. In the latter case the size of the food is highly significant. Infusorians cannot swallow algae that are larger than the diameter of the mouths of their shells. However, large monocellular and colonial algae equipped with long protuberances constitute as much as 90% of summer plankton. Therefore, regardless of the abundance of phytoplankton (whose biomass is almost two orders greater than that of the infusorians) an acut shortage of food is inevitable. In the absence of algal food the phytophagous infusorians switch over to bacteria consumption. The biomass of bacteria in the White Sea is 5 to 40 milligrams per cubic meter. Even if we assume that all species of bacteria are equally acceptable to the infusorians (but this is not quite the case - Gold, 1969), then considering the rather marked need of the infusorians for bacterial food and particularly for its initial concentration (Pavlovskaya, 1971 et al.), we may ascertain that a shortage [of food] is felt even in this case. It appears to us that this is precisely the explanation for the low density of tintinnids in the sea as compared with that observed in an experiment under optimal feeding conditions (the difference is of 2-3 orders !).

<u>Temperature</u>. Many tintinnids occur within a wide range of temperatures (Table 2, Fig. 2). However, each species successfully develops within narrower limits. On the whole, we have a typical picture of a divergence of niches. The boundaries of the optimal temperatures in vertical, seasonal and water area distribution fully coincide and agree well with the geography of the species. /500

	<ol> <li>Акваторнальное распроделение (температура слоя 0,5 м)</li> </ol>			З Сезонное распроделение (температура слоя 0,5 м)			
Виды шфузорий	і днапазон ветречаемости «	7 оптимальный диапезон	3 среди. опти- маль- ная	С диапазон встречаемости	ії оптямальный днапазон	б средн. слти- и1ль- и1ль-	
T. campanula H. subulata F. tarcikaensis C. ovata T. parvula P. denticulata T. beroidea P. obtusa T. nana T. jimbriata	$ \begin{vmatrix} 6, 0 - 19, 5 \\ 6, 0 - 19, 5 \\ 9, 0 - 19, 5 \\ 0, 0 - 19, 5 \\ 8, 5 - 18, 4 \\ 6, 0 - 18, 4 \\ 6, 0 - 18, 4 \\ 6, 0 - 18, 4 \\ 6, 0 - 18, 2 \\ 0, 0 - 12, 6 \\ 6, 0 - 12, 6 \\ 0, 0 - 12, 6 \end{vmatrix} $	$\begin{array}{c} 18,0-19,5\\ 16,0-19,5\\ 17,0-48,0\\ 14,0-18,0\\ 12,4-17,6\\ 11,2-16,0\\ 8,5-15,4\\ 8,3-8,7\\ 11,0-11,4\\ 12,3-12,6\\ \end{array}$	18,7 17,6 17,5 16,7 14,9 13,5 12,5 8,5 11,2 12,5	7,0-19,0 $7,0-19,0$ $12,0-19,0$ $8,6-19,0$ $7,0-18,0$ $-1,4-19,0$ $-1,4-16,7$ $-1,4-16,7$ $-1,4-12,0$	10,7-19,0 10,7-19,0 10,0-17,0 12,0-17,0 12,0-15,0 9,0-15,0 7,0-12,0 6,0-10,0 ?	18,0 15,0 17,0 16,5 12,0 9,5 8,0 ?	

## Thermal life conditions of the White Sea tintinnids

Ч	Ч Вертикальное распределение			5 Общие данима			
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$\begin{array}{r} 9,0-17,8\\ -1,2-17,8\\ 16,7-17,8\\ 11,5-16,0\\ 7,7-16,0\\ -1,2-16,0\\ 6,0-12,6\\ -0,4-12,5\\ 1,3-12,6\\ 1,5-12,6\end{array}$	$\begin{array}{c} 17,5-18,0\\ 17,5-18,0\\ 17,5-17,8\\ 15,2-16,0\\ 11,0-12,4\\ 8,0-12,6\\ 3,5-12,4\\ 7,7-11,0\\ 4,4-8,4\\ \end{array}$	17,8 17,8 17,6 15,6 11,7 10,5 10,3 9,4 6,4 ?		$\begin{array}{c} 16,7-19,5\\ 16,0-19,5\\ 16,0-19,0\\ 14,0-18,0\\ 11,0-17,6\\ 8,0-16,0\\ 7,0-15,4\\ 6,0-11,0\\ 4,4-8,4\\ -1,4-6,8 \end{array}$	18,1 17,7 17,5 15,0 14,3 12,0 11,2 8,5 6,4 2,7

Key to table 2:

1 - Species of Infusorian;

2 - Distribution over the water area (temperature of the 0.5 - meter layer);

3 - Seasonal distribution (temperature of the 0.5 - meter layer);

4 - Vertical distribution;

5 - General data;

6 - Range of occurrence;

7 - Optimal range;

8 - Average optimal.

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The Boreal species have optimums that are even higher than those of the Arctic-Boreal species and still higher than those of the Arctic species. The lowest temperature at which live infusorians have been found is  $-1.4^{\circ}$ C. At this temperature <u>T</u>. <u>fimbriata</u> attains the highest abundance, whole other species occur extremely rarely or not at all. Since we know of no cysts in tintinnids, we must assume that most important White Sea species can exist for a long time (several months) at below-freezing temperatures, and that their absence in winter samples is explained only by their low abundance. This has been proven for P. denticulata (Burkovskiy, 1973). Nor can it be ruled out that the populations of certain White Sea species perish completely during the winter and are restored in the spring by Barents Sea forms finding their way here with the current. At maximum temperature for the White Sea (about 24°C in shallow inlets of Kandalaksha Bay in the summer of 1972) the species <u>T</u>. <u>cam-</u> <u>panula</u>, F. taraikaensis and H. subulata were found in great abundance.

Salinity. In the White Sea, fluctuations in salinity are not as great as the fluctuations in temperature. Except for some strongly desalinated regions of Dvina and Onega Bays the salinity stays within the range of 23 to  $70^{\circ}/00$ . All the White Sea infusorians occur at this salinity. Only <u>T. fimbri-</u> <u>ata</u>, a brackish-water species, develops the most successfully when the salinity is low (about 15 to  $20^{\circ}/00$ ). Since the vertical and the seasonal changes in salinity and in temperature are interrelated, the relation to the salinity in most instances is determined by the relation to the temperature.

<u>Vertical distribution</u>. We studied the distribution by depth of 8 species of infusorians and observed a general tendency for tintinnid abundance to decrease with depth, reflecting a corresponding change in temperature and food. (fig. 3). Individual specimens of <u>P</u>. <u>obtusa</u>, <u>P</u>. <u>denticulata</u> and <u>H</u>. <u>subulata</u> occurred below 25 meters. The maximum depth these species penetrated was 100 meters. The upper 15 meters constituted the most densily populated layer; here

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Figure 2. Temperature niches of the White Sea tintinnids.

1 - <u>T</u>. fimbriata; 2 - <u>T</u>. nana; 3 - <u>T</u>. <u>obtusa</u>; 4 - <u>T</u>. <u>beroidea</u>; 5 - <u>P</u>. <u>denticulata</u>; 6 - <u>T</u>. <u>parvula</u>; 7 - <u>C</u>. <u>ovata</u>; 8 - <u>F</u>. <u>taraikaensis</u>; 9 - <u>H</u>. <u>subulata</u>; 10 - <u>T</u>. <u>cam</u>panula</u>; the optimal temperature is shaded in black.





1 - infusorians; 2 - temperature; 3 - bacteria; 4 - algae.

## Key to Fig. 3:

- 1 Depth in meters;
- 2 specimens per cubic meter;
- 3 infusorians;
- 4 temperature;
- $5 10^5$  specimens per millilitre;
- 6 bacteria;
- 7 milligrams per cubic meter;
- 8 algae.

the infusorians found the necessary food and suitable temperature. Six out of eight species reached their maximum abundance in the 0-5-meter layer (fig. 4). These were the most thermophilic forms. The position closest to the surface was occupied by <u>T</u>. <u>campanula</u>, followed by <u>H</u>. <u>subulata</u>, <u>F</u>. <u>taraikaensis</u>, <u>C</u>. <u>ovata</u>, <u>T</u>. <u>parvula</u> and <u>T</u>. <u>beroidea</u>. <u>P</u>. <u>denticulata</u> reached its greatest density in the 5 to 10 meters layer, while <u>P</u>. <u>obtusa</u> reached it somewhat deeper. The vertical distribution of the tintinnids was undoubtedly tied to their relation to the temperature. The surface layer, rich in food is utilized best by thermophilic forms, and least by phychrophilic ones. In shallow areas, where vertical stratification is little evident, the tintinnids manifest a distribution pattern that is similar and more uniform with depth. Material for the study of the seasonal abundance of tintinnids was collected in just such a place. We expected that the divergence in time of ecologically close species would be greater in proportion as it had less chance to appear in space.



Figure 4. Vertical distribution of tintinnids

1 - <u>T. campanula</u>; 2 - <u>H. subulata</u>; 3 - <u>F. taraikaensis</u>; 4 - <u>C. ovata</u>; 5 - <u>T. parvula</u>; 6 - <u>T. beroidea</u>; 7 - <u>P. denticulata</u>; 8 - <u>P. obtusa</u>. The abundance of each species is taken as 100%.

Key to Fig. 4: 1 - depth, in meters.



Figure 5. Seasonal distribution of tintinnids

1 - <u>P. obtusa;</u> 2 - <u>P. denticulata;</u> 3 - <u>C. ovata;</u> 4 - <u>F. taraikaensis;</u> 5 - <u>H. subulata;</u> 6 - <u>T. campanula;</u> 7 - <u>T. beroidea;</u> 8 - <u>T. fimbriata;</u> 9 - temperature. Key to Fig. 5:

1 - Density of infusorians, specimens per cubic meter;2 - Months.

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Seasonal distribution. In the course of a year considerable changes in the abundance of tintinnids are observed. With the exception of T. fimbriata all the species reach their maximum density in the summer-fall period. A sharp increase in tintinnid abundance in plankton usually appears in June at a temperature of 6 to 8°C. Until then the density of infusorians has not exceeded 100 specimens per cubic meter. P. denticulata, P. obtusa and T. beroidea occasionally occurred. During the warm period of the year a change of the dominant species takes place. Most likely this change is due to a combination of changing conditions. We succeeded in tracing the relation to temperature. Psychrophilic species multiply first. At a temperature of 8°C P. obtusa reaches its maximum (fig. 5); P. denticulata does the same later at a temperature of 14°C. Further increase in temperature leads to rapid multiplication first of C. ovata (16°C.), then of F. taraikaensis (17°C.), H. subulata and T. campanula (19°C.). At this time P. obtusa disappears from the samples and the population of P. denticulata decreases sharply (by two orders). With a drop in temperature

we observe a gradual decrease in the proportion of thermophilic species and an increase in that of psychrophilic species. In the middle of September <u>T. beroidea and P. denticulata</u> form the bulk of the tintinnids. At the end of the fall their abundance drops and later only individual specimens may be found in the samples. In December and January <u>T. fimbriata</u> is observed in great abundance (up to 12 thousand specimens per cubic meter). This is the only species attaining its maximum abundance in the winter at a negative temperature (-1.4°C.).

Distribution over the water area. Some of the species that we studied occur widely over the water area (P. denticulata, H. subulata, C. ovata, T. beroidea), others are restricted to certain areas (T. campanula, F. taraikaensis, P. obtusa), and finally, still others are limited to a rather narrow region (T. nana, at Gorlo [or The Strait], T. fimbriata, - Dvina Bay: T. parvula, /503 entrance to Onega Bay). The differences are further increased by the irregular density distribution of populations forming rather large and spotty accumulations. As a rule, each species has only one spot (P. denticulata has two). In proportion to distance from the spots the density decreases gradually, sometimes, however, rather abruptly (T. fimbriata, P. obtusa, T. nana, T. taraikaensis). The size of the spots varies from species to species within a range of 10 to 25% of the observed population area, but they contain from 30 to 70% of the total population. The degree of population dispersion may be estimated using the niche width equation. High values of the factor indicate that the species has an extensive and uniform distribution, while low values indicate that the distribution is limited and compact. The following values have been obtained: P. denticulata - 30.0; C. ovata - 23.2; T. beroidea - 21.1: H. subulata - 19.6; T. campanula - 12.4; T. parvula - 9.6; F. taraikaensis - 5.9; T. nana - 4.9; P. obtusa - 4.2; T. fimbriata - 2.0). A population of the first type is more /504 dispersed and its niche is wider; a population of the second type is more

compact and its niche is narrow. The first type represents the "generalist" and the second, the "specialist".



Figure 6. Location of the population nuclei of various tintinnid species (I) and the distribution of the temperature of the surface layer (0.5 meter) in the White Sea (II).

1 - F. taraikaensis; 2 - T. campanula, 3 - H. subulata; 4 - C. ovata; 5 - P. denticulata; 6 - T. nana; 7 - T. fimbriata; 8 - T. parvula; 9 - T. beroidea; 10 - P. obtusa.

Key to Fig. 6:

1 - Belomorsk;

2 - Arkhangel'sk/Archangel/.

s,

Fig. 6, I, shows spots (nuclei) of different populations. Their boundaries are drawn with allowance not only for absolute, but also relative density. The dispersal of nuclei over the entire White Sea is worth noting. A comparison of the data in Figs. 2 and 6 indicates that this dispersal takes place in full agreement with the requirement of the species for optimal tempera-Populations of psychrophilic species form accumulations in the Gorlo ture. and in Dvina and Onega Bays, while thermophilic species accumulate in Kandalaksha It is obvious that infusorians accumulate in corresponding regions not Bay. because of migration, but due to an intensified reproduction rate under favourable conditions. We may assume that with a change in conditions the distribution pattern of the infusorians also changes. Thus, the distribution picture recorded by us reflects merely a single moment in the development and interaction of the populations.



<u>Figure 7.</u> Interaction of infusorian species. A dot corresponds to each pair of factors  $(a_{ij} \text{ and } a_{ji})$ . 31 combination pairs are presented, indicating the highest values of the factors;  $1 - \underline{T}$ . <u>nana</u>;  $2 - \underline{T}$ . <u>fimbriata</u>;  $3 - \underline{T}$ . <u>parvula</u>;  $4 - \underline{T}$ . <u>beroidea</u>;  $5 - \underline{T}$ . <u>campanula</u>;  $6 - \underline{C}$ . <u>ovata</u>;  $7 - \underline{P}$ . <u>denticulata</u>;  $8 - \underline{H}$ . <u>subulata</u>;  $9 - \underline{F}$ . <u>taraikaensis</u>;  $10 - \underline{P}$ . <u>obtusa</u>.

---- C.a × + // + × | × Hs \_\_\_\_\_ I.0 \_\_\_\_\_ P.0

Figure 8. Basic interactions of the tintinnid species. The arrows indicate the direction and force of the action. The diagram shows abbreviated Latin names of the species (see Fig. 7 for the full names).

If we know the distribution of the individual species, we can easily estimate their interaction. Forty-five paired combinations are possible for ten species. Most of the pairs interact very poorly or not at all (fig. 7). They occupy the left bottom square of the graph. These species strongly disagree in their choice of habitats. Ten pairs manifest interaction of medium strength (upper left and bottom right squares). Finally, four pairs interact rather strongly (the upper right square). Fig. 8 shows the basic interactions among the species within the confines of the water area studied. The diagram is set up for easy comparison with fig. 5. The length of the arrows corresponds to the value of the interaction factors. Differences in the factors a and a, indicate different competitiveness of the species, and their algebraic sum gives an indication of the direction and force of the competition stress. Let us illustrate the situation using the example of the occurrence of three species with similar temperature optimums and therefore occupying the same region of the White Sea Basin, namely its western portion. The species F. taraikaensis hinders the westward progress of the species T. campanula; the species F. taraikaensis and T. campanula hinder the progress of the species

16

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H. <u>subulata</u>. By pursuing the interpretation of the picture, we come to the conclusion that the occurrence of each species is curbed by one or several other species with similar habitat. The competitiveness of species is directly related to the width of the niche. The "generalist" species are less competitive than the "specialist" species. <u>P. denticulata</u>, which has the widest niche, suffers the heaviest pressure from competition and is pushed away to a zone, where no other species is capable of successful development. Evidently these conditions are not optimal for <u>P. denticulata</u> itself, and therefore, its abundance is not so great at that time. Thus, we have received an answer to the question which we asked in a preceding article (Burkovskiy, 1974), but which we could not solve at that time due to the lack of data on the distribution of other species.

A simultaneous successful development of closely related species is possible owing to the distribution between them of food resources, or by division of the biotope, or by combination of these two mechanisms. The first of these operates among intensely interacting species. The distribution of food resources is realized in the case of the tintinnids by a double method: by their joint use and by food specialization. The fact that there really is a specialization is indicated, in addition to data on the contents of alimentary vacuoles, by the differentiated correlative relation between the distribution of the tintinnids and their food (table 3). Large infusorians basically feed upon algae, and the smaller ones, upon bacteria. It is possible that selectivity is more refined and that different species of tintinnids feed upon different species of algae and bacteria. Gold's experiments (Gold, 1970) show that it is not a matter of indifference to T. beroidea which bacteria constitute the composition of the food medium. The second mechanism is observed in species which relate in different ways to the entire complex or, sometimes, to one of the factors of the medium. Very often these are taxonomically close species

(for example, species of the genus Tintinnopsis).

Fig. 9 presents general data on the distribution of the abundance and biomass of tintinnids in the White Sea. Both factors increase in the western part of the basin and decrease in the eastern and northern parts. This, as we now know, is caused by the effect of a complex of factors, the most important of which are the temperature, food and competition. A number of common factors in tintinnid distribution is explained by the effect of hydrodynamic factors. Particularly noticeable is the effect of the current along the Terskiy coast of the Kola Peninsula.

#### Table 3.

Relation between the distribution of infusorians and their food. Correlation factors\*)

I. Виды инфузорий	<b>Ъ</b> Пища		11	ż. Tinuja		
	3 водоросли	4 бактерия	Виды инфузорий	3 водоросли .	/ бактерии	
P. denticulat.a F. taraikaensis P. obtusa T. campanula C. ovata	+0.52 +0.51 +0.44 +0.33 -0.05	$\begin{array}{c c} -0.02 \\ -0.26 \\ -0.19 \\ -0.04 \\ -0.84 \end{array}$	T. jimbriata H. subulata T. nana T. parcula T. beroidea	$-0.05 \\ -0.09 \\ -0.02 \\ -0.09 \\ \div 0.07$	+0,81 +0,54 +0,43 +0,23 +0,23	

\*) Factor values less than 0.20 are not reliable.

Key to the table:

- 1 Species of infusoria;
- 2 Food;
- 3 algae;
- 4 bacteria.



Figure 9. Distribution of the density (I) and biomass (II) of tintinnids in the White Sea in the 0-25 meter layer. Density in thousands of specimens per cubic meter, Biomass in milligrams per cubic meter.

Key to fig. 9:

1 - Kem';

2 - Arkhangel'sk/Archangel/;

3 - Chupa.

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#### ECOLOGY OF TINTINNIDA (CILIATA) OF THE WHITE SEA

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#### Summary

20 species of tintinnids were registered in the White Sea fauna, among them 10 mass species. The average density of ciliates in the layer 0-25 m amounts in summer to 43,000 specimens per 1  $m^3$  and the biomass to 3.8  $mg/m^3$  (net collections). The most species develop in the layer 0-10 m, the population density of ciliates decreases with the depth. The change of predominant species occurs during the year in accordance with the ternperature changes. The most species attain their highest density in summer. The density of tintinnids in winter amounts to 10-100 specimens per 1 m<sup>3</sup>. The distribution of cillates in an aquatorium follows the spotted pattern. It depends on temperature, food, competition and some other environmental factors.