Variability of Parafavella denticulata in the White Sea

/1277*/

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A comparative study of the structure of the shells and body of
Parafavella showed that only 1 species, P. denticulata Ehrenberg (K. and
C.) inhabited the White Sea. All the other forms described earlier as
independent species are but variations of this highly variable species.
This paper contains a detailed analysis of the populational, seasonal
and biotopic variability of P. denticulata, as well as the first descrip-
tion ever of cyclomorphosis in pelagic marine ciliates.

The genus Parafavella includes the marine tintinnids with a

symmetrical hexagonal structure of the shell walls. The taxonomy of

the genus, which is based exclusively on the differences in the shape

of the lorica, has hardly been developed. There is no unanimous approach

to the morphological criteria of the species, and the exact number of

species in this genus is still unknown. The available literature, which

includes a little over 40 works, is basically faunistic and contains

numerous inaccuracies in the identification and description of the ciliates.

*The numbers in the right-hand margin are the pages of the Russian text
- translator.

It presents a distorted picture of the geographical distribution of this, most likely, Arctic-boreal genus. The data on the variability of the ciliates, which could shed some light on the taxonomy of the genus, are fragmentary (Schulz, Wulff, 1927; Wulff, Schulz, 1929; Strelkov, 1953). The study of the variability of ciliates is also of interest to general biology, particularly populational biology.

Nine forms of Parafavella have been noted for the White Sea by different authors (Pertsova and Chibisova, 1970). The most common of these are Parafavella denticulata (Ehrenberg) Kofoid and Campbell, P. media (Brandt) Kofoid and Campbell and P. gigantea (Brandt) Kofoid and Campbell, which differ mainly in the size of the lorica. Other forms are encountered very rarely [P. robusta (Jörgensen) K. and C., P. cylindrica (Jörgensen) K. and C., P. edentata (Brandt) K. and C., P. rotundata (Jörgensen) K. and C., P. subrotundata (Jörgensen) K. and C. and P. temus Wulff]. At first these were considered as variations of one and the same species P. denticulata Ehrenberg. However, they were later singled out as independent species (Kofoid and Campbell, 1929) on insufficient grounds. Since then, despite a number of strong objections (Schulz, Wulff, 1927, 1929), these forms became established as species, giving cause for the unjustified elevation of the rank of certain other variations.

Material and Methods

The material for the study was collected in 1971-1972 in different areas of the White Sea (Fig. 1) with a quantitative plankton net made of bolting cloth No. 77 having an inlet diameter of 19 cm. A net made of this cloth catches all the size groups of Parafavella and even smaller tintinnids (Ptychocylis, Tintinnopsis, Stenosemella and others). At

stations where the depth did not exceed 25 m, total samples were taken

from large depths (0-25 m layer) (depths of stations given in Table 1).

The vertical distribution of ciliates in the open water was studied with

the help of a closing net of the type described above in the 0-5, 5-10,

10-15, 15-20, 20-25, 25-50, 50-100 and 100-200 m layers. In winter,

due to the very low numbers of ciliates, a series of 15-60 catches was   /1278/

carried out at each station so that not less than 10 m^3 of water was

filtered. This enabled us to collect sufficient material for studying

the variability and greatly increased the reliability of the winter

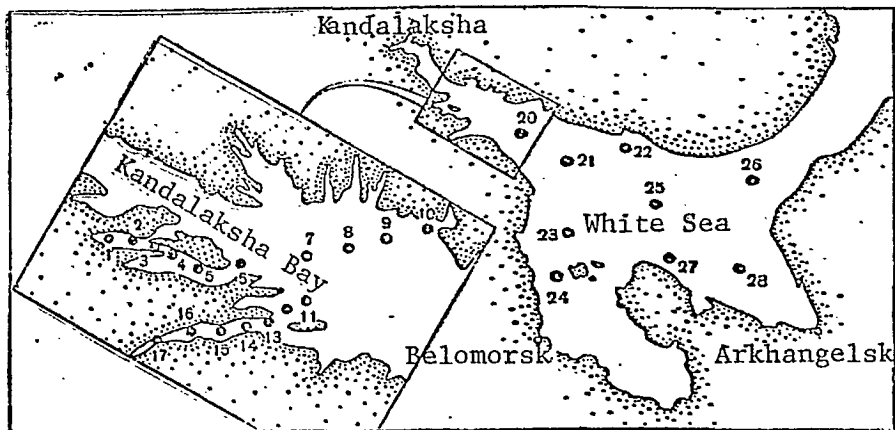quantitative data. The material was fixed in a 4% solution of formalin.

Figure 1

Study area

1-28 - station numbers, the places
at which the material was collected

The ciliates were counted under a binocular lens, not less than 0.1 of the entire sample being viewed. 100-200 specimens were selected from each sample in order to study the variability of the lorica. Some 14,300 specimens were examined in all. The ciliates were studied live and in preparations stained with hemalaun[*] and impregnated with silver after Shatton and Lvov in the modified version of Corliss (1953). The material was processed statistically. All the data are statistically reliable (according to the upper confidence level) unless specified otherwise. We have also made use of 1970-1971 phytoplankton data, kindly contributed by L.A. Konoplya, a fellow worker of the hydrobiology department of Moscow University, to whom we are deeply grateful.

Species affiliation of White Sea Parafavella

The material of 1971-1972 was found to contain all the White Sea forms known to us earlier, as well as shells identical to those of P. promissa Hada and P. ventricosa Jörgensen. Thus, we found 11 forms in all (Fig. 2). The most abundant were P. denticulata, P. media, P. gigantea and P. robusta. The others constituted not more than 2-3% of the total numbers. A series of gradual transitions exists between all the types of lorica shown in Fig. 2. For example, we observe a gradual transition from the lorica with a developed barb (phenotypes denticulata, media, gigantea and others) to forms with a highly reduced barb (phenotype subrotundata) or barbless forms (phenotype rotundata), from a conical shell (most phenotypes) to a cylindrical one (cylindrica) or to the ventricosa-type

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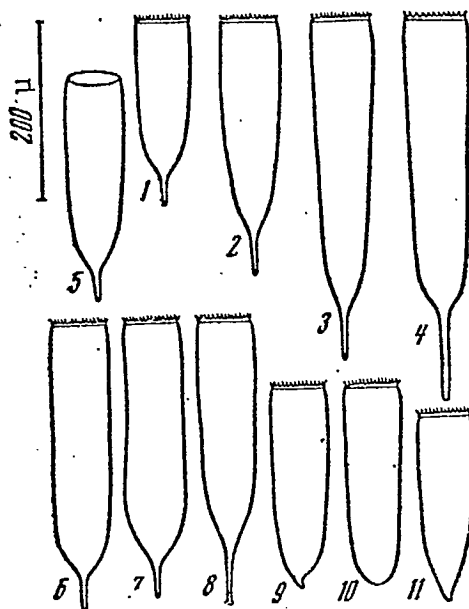[*]Translator's note. Transliterated from the Russian; no other suitable equivalent available.

Figure 2

The basic phenotypes of P. denticulata
in the White Sea

1 - denticulata, 2 - media, 3 - gigantea,
4 - robusta, 5 - edentata, 6 - cylindrica,
7 - ventricosa, 8 - promissa, 9 - subrotundata,
10 - rotundata, 11 - tenuis

shell. It is absolutely impossible to draw a line between forms like

denticulata, media and gigantea, which are claimed to differ when they /1279/

reach their average size. The form promissa does not stand alone either.

All the transitions from the entirely normal conical barb to the cylindrical

one ending with a cap can be observed. The phenotype robusta is distinguished

by the large size of its lorica, strong barb, sturdy denticles and thick walls.

However, there also is a series of gradual transitions to other forms in this

phenotype as well, as we shall later see. Finally, the absence of denticles

in certain shells, as rightly pointed out by numerous authors in the past

(e.g. Meunier, 1910), is the result of some injury, and so cannot serve as a

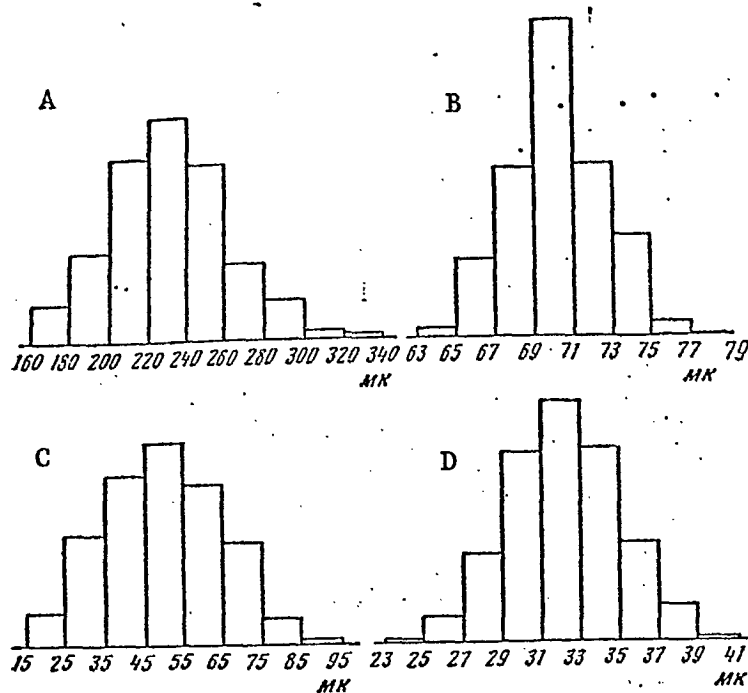basis for distinguishing these forms as independent species.

Figure 3

Histograms of the frequency of occurrence
of certain parameters of the P. denticulata
lorica in the 1971 population (July, stations
1-17)

A – length of vase*, B – diameter of vase,
C –. length of barb, D – number of denticles.

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*Revisor's note. Taken directly from the original Russian vaza.

The absence of discontinuity in the variability series of the

lorica of White Sea Parafavella indicates that it is groundless to single

out these forms as independent species. This is also substantiated by

the nature of the frequency distribution of the basic characters. In

representative selection, it always has the form of a normal single-peak

symmetrical distribution (Fig. 3). Another important argument which

points to the fact that these forms belong to the same species is the absolutely identical structure of the ciliate itself, regardless of the type of lorica. All these facts confirm the view of earlier authors who considered these forms as variations (phenotypes) of P. denticulata Ehrenberg.

Structure of the lorica of P. denticulata and its

variability

The lorica is of organic material, transparent, with symmetrical hexagonal double walls, usually conical in shape (Fig. 4). The anterior broad end has an opening (mouth) topped by a crown bearing numerous triangular denticles. Below the base of the denticles, the lorica at first broadens slightly (diameter of the mouth is 3-6 μ less than the maximum diameter of the lorica) and then gradually narrows, drawing out into an aboral barb at the posterior end. The distance from the mouth to the surface through the maximum diameter averages approximately 0.1 of the length of the vase (the main part of the lorica). The vase cavity frequently extends /1280/ into the barb cavity. The barb is smooth, not hexagonal, sometimes vestigial or lacking. The posterior end is always closed, the mouth being the only connection between the shell (lorica) cavity and the medium. The ciliate fastens itself to the inner wall in the posterior third of the lorica by means of a long and highly contractile stalk. The body of the ciliate is symmetrically conical, poorly contractile, 80-120 x 60-80 μ in size. The adoral zone of membranelles in tintinnids usually consists of 22-24 membranelles. The cytoplasm is granular, opaque, vacuolated, with a large number of food inclusions (bacteria, dinoflagellates, zooflagellates and diatoms), 2 ellipsoidal macronuclei and 2 micronuclei.
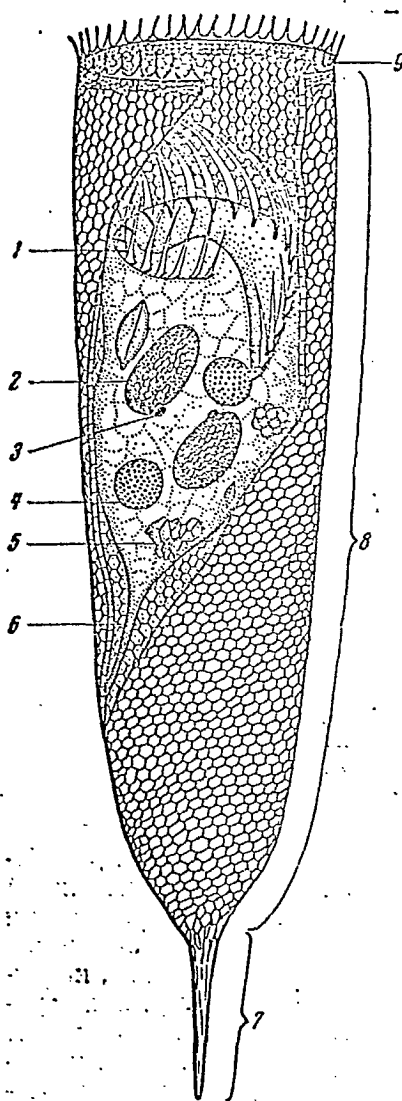
Figure 4

P. denticulata (combined drawing):
living specimen, in formalin, stained
with hemalaun*, impregnated with silver)

1 - adoral zone of membranelles,
2 - macronucleus, 3 - micronucleus,
4 - digestive vacuole, 5 - grit,
6 - stalk, 7 - barb, 8 - vase,
9 - crown with denticles

*See previous footnote - transl.

The lorica of P. denticulata is highly variable, primarily in its shape. The shells are mostly cone-shaped (from 97 to 99%), but may sometimes be cylindrical (1-3%) or widened from behind (less than 0.1%). As mentioned earlier, gradual transitions exist between these types. The configuration of the shell frequently alters, a more or less clearly defined narrowing being observed in the middle portion. This type of narrowing is encountered in up to 15% of the small shells and up to 60% of the large ones.

The aboral barb may be long or short (even vestigial), straight or curved, conical or cylindrical, with or without a cavity, thin or thick, blunt or sharp. The number of denticles along the edge of the mouth varies from 22 to 42, the average approximating 30. The denticles range from weak to strong ones.

The symmetrical hexagonal structure of the shell walls, which is a generic character, undergoes very little change. The observed variations involve the size of the hexagonal shells (from 2.7 to 3.6 µ), the distinctness of the pattern, and the thickness and transparency of the shell.

Linear characters, such as length and the maximum diameter of the vase, as well as the length of the barb, vary considerably. The diameter of the vase is the least variable (variation coefficient 3-5), and the length of the barb is the most variable (CV = 15-25). The length of the vase (CV = 10-15) and the number of denticles (CV = 10-15) occupy an intermediate position.

The simple construction and relatively large size of the shell, combined with excellent storage life in standard stabilizers (fixatives),

and requiring no complicated cytological methods (as is the case when

studying the ciliate itself) make it possible to process a vast amount

of material, making it extremely convenient to study the populational

structure of the species. True, in this case, not the body of the

ciliate but instead, its derivative structure is studied, the latter

being more variable and keenly sensitive to the surrounding medium. /1281/

However, the second circumstance acquires a special significance, as

it enables us to detect even the slightest changes in the structure of

a population.

Seasonal variability of P. denticulata

(cyclomorphosis)

Quantitative and qualitative changes occur in a population

throughout the year (see Fig. 5-7). During the second half of summer,

when food is most abundant and moderate temperature relatively stable,

the population of P. denticulata reaches its maximum density and consists

primarily of small individuals (phenotype denticulata). A little later,

as the temperature drops to 6-8°C, the numbers of ciliates sharply

diminish and a noticeable increase in the average size of the lorica

is observed (phenotype media). A further drop in temperature to 3-5°C

results in the formation of gigantea-type forms at first, and forms

intermediate between gigantea and robusta later. The latter are

characterized by a vase greater in diameter than that of gigantea, and

by comparatively thick walls though still very weak denticles, and a

thin, but long aboral barb with a weakly defined cavity. In October,

when the temperature drops below 1-2°C, the entire population consists

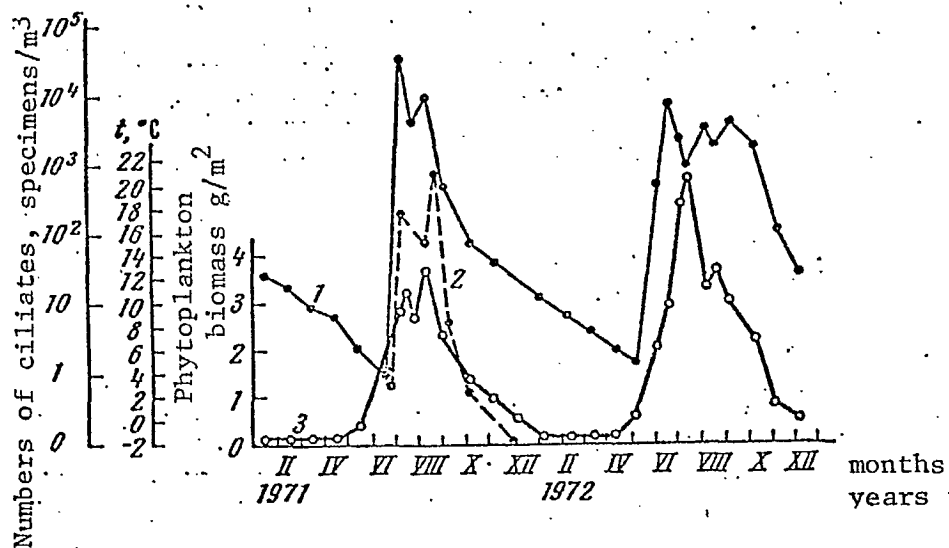of ciliates with large, thick-walled shells bearing a sturdy barb and

Figure 5

Fluctuation in the numbers of
P. denticulata in 1971-1972.

1 - numbers of ciliates,
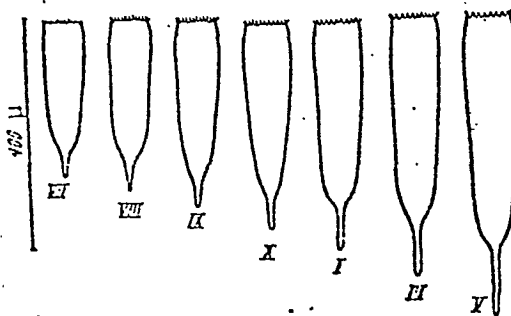2 - phytoplankton biomass,
3 - temperature

Figure 6

Seasonal changes in the lorica of
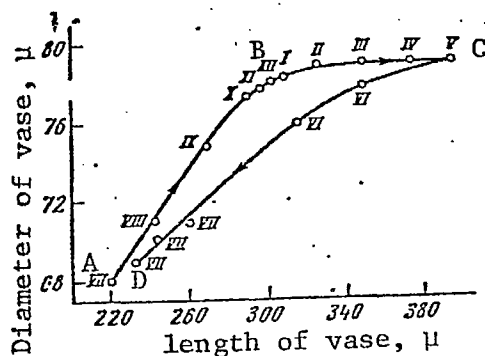P. denticulata

Roman numerals denote the months.

Figure 7

Curve of change of average size
of vase (ABCD) during the year

Roman numerals denote the·months;
the arrows, the direction of the
changes

strong triangular denticles (phenotype robusta). In the period following   /1282/

that, which lasts 6-7 months, the ciliates live in conditions of freezing

temperature (down to -1.5°C) and an acute shortage of food (Fig. 5). By

the end of the period of hydrologic winter, the numbers of ciliates

diminish to 1-2 specimens/m^3, the size of the shell increasing even more

(Fig. 6-7). The growth of the shell ceases only in May–June, when the

temperature of the water goes up to 3-4°C. This period is characterized

by extensive development of the phytoplankton and a fairly rapid increase

in the numbers of ciliates. Over a period of several days, the density

of the population increases by several thousand times (Fig. 5). From this

point on, we observe the first signs of metamorphosis of the winter robusta-

type forms into summer forms of the gigantea--media--denticulata type,

this process being quicker than in autumn and in the reverse order. At

first, the walls of the shell become thinner, the hexagonal structure less

pronounced, and the denticles around the mouth weaker. Then the barb

becomes shorter and thinner, and its cavity less defined. And only then,

does the shell decrease in size. Thus, the metamorphosis of the phenotype

<u>robusta</u> into <u>gigantea</u> takes place over a period of 10-20 generations.

In July, all the ciliates have the typical thin-walled shell with a short,

thin barb and weak denticles. However, the vase still continues to

diminish in size up to the middle of August. And so, throughout the year,

the loricae of <u>P</u>. <u>denticulata</u> undergo complex metamorphoses, similar to

the cyclomorphosis of freshwater rotifers, water fleas, peridinia and

other organisms (Hutchinson, 1967). The only difference is that ciliates

do not undergo neomorphosis; only the size of the existing structures

alters. It is still unclear whether cyclomorphosis in ciliates is an

external manifestation of adaptive physiological changes within the

organism, which are caused by a change in conditions (primarily temperature

and the food regime), or whether it is also the process of population

maturation. From the point of view of the second assumption, it is

particularly interesting to note the change in shell size on the curve ABC

(Fig. 7) which can be compared with the typical curve of individual growth

of the animals. In the given case, the generations replacing each other

behave as individuals of multicellular animals.

Fluctuations in population diversity are observed throughout the

year; we are unable, however, to establish any system in the nature of

these changes. We were also unable to detect any noticeable seasonal

differences in the structure of the ciliate itself. Apparently, this requires more refined cytologic and cytochemical methods.

Biotopic variability

The White Sea coastline is highly indented into a number of shallow bays. Their hydrologic and hydrochemical regime is determined largely by the abundant continental runoff and the close contact with the sea bottom, and differs from that of the open sea. As we move farther out to sea, we observe a gradual change in the composition of the P. denticulata population (Table 1). Large forms predominate in the innermost parts of the bay (stations 1 and 17). Farther out, the average size of the ciliates gradually decreases (stations 2-5 and 16-12), reaching the minimum in the open sea (stations 6-11). It should be stressed that the gradual change in the average size does not occur as a result of the change in the ratio of small and large forms (which would indicate that isolated -phenon[e]s or -morphs existed), but as a result of a real increase in the size of the shells in the bays. This is indicated by the exceptionally constant indices of diversity with a regular change in mean values. A noticeable decrease in diversity is characteristic only of that part of the population which is farthest /1283/ from the open sea (stations 17 and 1).

The regular changes relate not only to the size and proportions of the shell, but to certain other characteristics as well. We observe a sufficiently reliable, though insignificant increase in the length of the barb and a decrease in the number of denticles in the forms encountered in the innermost part of the bay. There is also an increase in the percentage of shells with a clearly defined median narrowing. It is

Table 1.

Biotopic (horizontal) variability of <u>Parafavella</u>
<u>denticulata</u> shell*

Sta-tion No.	Depth m	Hori-zon, m	Numbers of ciliates		Length of vase	Diameter of vase	Length of barb	Number of dent-icles	Median narrowing	
			in 1m³	under 1m²					pre-sent	lack-ing
1	6	0—6	1080	6 480	290,0±2,2	72,5±0,2	51,8±0,9	29,5±0,3	69	31
2	7	0—7	1710	12 040	252,6±2,8	71,6±0,2	50,1±1,0	31,0±0,3	53	47
3	15	0—15	1880	28 650	239,7±2,9	71,0±0,2	49,6±1,1	31,4±0,3	51	49
4	50	0—25	2020	61 000	232,3±2,9	70,0±0,2	49,2±1,1	31,7±0,3	47	53
5	75	0—25	2670	66 750	227,2±2,8	69,8±0,2	48,1±1,1	32,4±0,4	45	55
6	120	0—25	3370	84 250	220,1±2,7	69,5±0,3	46,5±1,1	33,1±0,5	40	60
7	215	0—25	3200	79 750	220,6±2,8	69,6±0,3	47,2±0,9	33,4±0,4	38	62
8	280	0—25	3040	75 800	220,8±2,8	69,8±0,3	47,5±1,0	33,7±0,4	31	69
9	240	0—25	3020	75 500	221,8±2,8	69,5±0,3	47,3±0,9	33,2±0,4	28	72
10	60	0—25	2980	74 500	222,5±2,4	68,9±0,3	47,1±0,9	32,6±0,4	22	78
11	55	0—25	2170	54 625	221,3±2,8	69,5±0,3	47,3±1,1	31,9±0,4	27	73
12	40	0—25	1960	49 000	232,7±2,8	70,0±0,3	49,4±1,1	31,4±0,4	34	66
13	35	0—25	1740	43 625	240,0±2,8	70,6±0,3	52,8±1,1	31,0±0,4	37	63
14	30	0—25	1680	42 000	248,2±2,8	70,9±0,2	53,1±1,1	30,8±0,3	38	62
15	20	0—20	1730	34 700	252,7±2,7	71,3±0,2	53,4±1,0	30,7±0,3	40	60
16	15	0—15	1740	26 100	257,6±2,6	71,6±0,2	53,6±1,0	30,5±0,3	54	56
17	8	0—8	1280	10 240	288,8±2,1	72,4±0,2	54,3±0,8	29,4±0,2	63	37

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*100 specimens were measured in each case; the variation coefficient (CV) fluctuates from 7.2 to 12.6 for vase length, 2.8-4.0 for vase diameter, 6.2-23.0 for barb length and 8.3-13.6 for the number of denticles.

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of utmost importance to note that all these changes appear to the same /1284/ extent and parallelly both in Rugozero Bay and in Chupa Bay (compare stations 1-6 and 17-11). In both cases the differences between the phenotypes are due to the heterogeneity of the habitat. The regular change of phenotypes represents the corresponding reaction of the organisms to the change in the surrounding medium. The observed variability, therefore, is biotopic variability.

Table 2.

Depth (vertical) variability of _Parafavella_
denticulate shell*

Horizon, m	Temperature, °C	Salinity, ‰	Phytoplankton, mg/m^3	Numbers of ciliates in 1 m^3	Length of vase	Diameter of vase	Length of barb	No. of denticles
0—5	16,3	25,1	327	3200	217,8±1,6	70,0±0,2	52,5±1,0	30,9±0,2
5—10	13,2	25,4	220	3000	218,1±2,3	70,2±0,2	52,7±1,0	29,9±0,3
10—15	10,3	26,1	45	810	211,5±2,0	69,3±0,2	51,7±1,0	29,8±0,3
15—20	6,8	26,6	13	450	210,0±2,0	69,4±0,2	52,1±1,0	30,5±0,3
20—25	4,1	27,2	7	400	211,5±1,5	69,7±0,2	51,1±0,9	29,7±0,3
25—50	1,2	27,8	5	300	209,0±1,7	69,4±0,2	50,4±0,8	29,7±0,3
50—100	—0,5	29,5	1	80	216,9±1,7	70,5±0,2	51,4±1,0	29,9±0,3
100—200	—1,5	30,7	—	10	228,0±1,8	70,7±0,2	50,0±1,0	31,2±0,3

*100 specimens were measured in the 100-200 m layer, and 200 in each
of the other layers; CV 7.4-10.5 for vase length, 2.4-3.0 for vase
diameter, 15.8-20.0 for barb length and 7.0-9.0 for the number of
denticles.

Table 3.

Relationship between certain shell parameters*

Population	n	Indices					
		Length and diameter of vase			Length and diameter of barb		
		η	t_η	t_c	η	t_η	t_c
Summer (July)	471	0,24	9,7	2,7	0,23	10,1	3,8
Winter (January)	429	0,14	8,3	8,8	0,16	7,8	6,6

*n – number of specimens, η – correlation ratio, t_η – significance
test of correlation ratio, t_c – test of curvilinearity.

Biotopically different parts of a population differ significantly in the seasonal range of variability and change in abundance (Figs. 8 and 9). Considerably greater changes occur throughout the year in the open sea (centre of a population) than in the bays (periphery of a population). For example, the average shell dimensions (station 6) range from 216 x 68 µ to 345 x 78 µ, whereas in the bays (station 1) they range from 240 x 69 to 330 x 78 µ. Cyclomorphosis in biotopically different parts of a population progresses at different rates and varying intensity, which is apparently due to the physiological heterogeneity of a population.
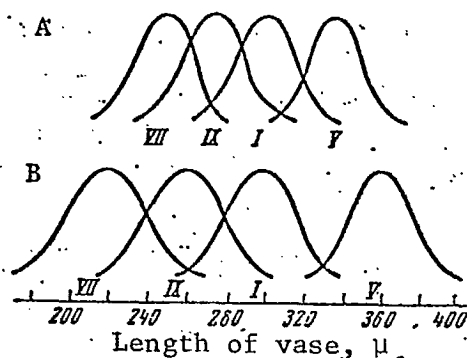

Figure 8

Variability of a P. denticulata shell in the central (A) and peripheral (B) parts of the population
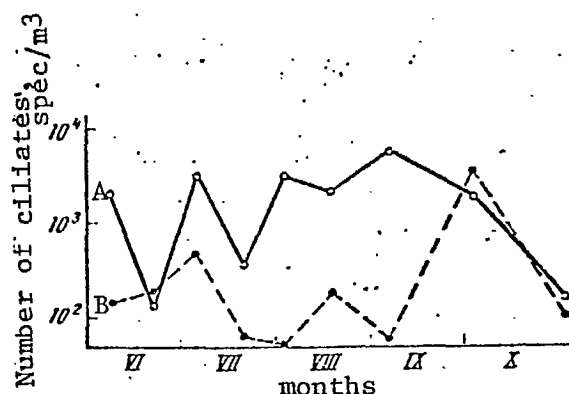
Roman numerals - months; A - station 6; B - station 1

Figure 9

Pattern of change in the numbers
of P. denticulata in the central
(A) and peripheral (B) parts of
the population

A – station 6; B – station 1

The results obtained from a study of the vertical varibility of

P. denticulata were unexpected. Judging by the abrupt change in temper-

ature (from 15-20° to -1.5°C), salinity from 25 to 31 ‰) and phytoplank-

ton biomass in the layers, one would assume there would be a corresponding

significant change in the structure of the population. However, this

is not the case, as seen in Table 2. We observe only a gradual decrease

in numbers as the depth increases; 96-98% of all the Parafavella inhabit

the photosynthetic, 0-25 m layer. A prominent point is the homogeneity

of the population. Only in extreme conditions (very low or high temper-

atures) do we observe a slight increase in the length of the shell. As

for the variation coefficients, they remain unchanged, or else the change

is not uniformly regular. In the 1971 material, the variation coefficients

for shell diameter, barb length and the number of denticles increase

with the depth, while the diversity indices for shell length show the

opposite tendency. It should be noted that on the whole, the _Parafavella_

shell is in itself a poorly co-ordinated system.

Table 3 gives an idea of the nature of the correlation between

certain linear parameters of the shell. Thus, we see that the correlation

between the characteristics is extremely weak and curvilinear. The

correlation is somewhat stronger in the small forms and weaker in the /1285/

large ones. It is stronger in the summer forms, is on the border of what

roughly could be called a rectilinear correlation, and is weaker in the

winter forms (a significantly curvilinear correlation). The superposition

of the correlation lattices of the winter and summper populations produces

a single curvilinear correlation, so that the curve of regression of the

winter population turns out to be the exact continuation of the curve of

regression of the summer population (more proof that these phenotypes

belong to the same species). It is believed that the weak correlation

between the different characters is one of the causes of the great

variability of _Parafavella_ shells.

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