

Efficiency of the Transport System of the Hydroid *Dynamena pumila* (L., 1758) under Different Abiotic Impacts

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Abstract—In the article, the efficiency (range and volume) of the transport of food particles suspended in hydroplasm along the stolon of the colonial hydroid *Dynamena pumila* inhabiting the littoral is determined with respect to four environmental factors: the temperature (10, 15, 20, 25, 28°C), salinity (26, 20, 15, 10‰), air exposure (duration 5, 10, 20, 30 min), and the presence or absence of water exchange. The capacity for efficient transport is determined based on the estimated length of local hydroplasma flows that form a chain continuous integral hydroplasmic flows. Local flows covering one or two stolon modules are theoretically sufficient for the generation of joint extended hydroplasmic flows and are thus equally represented for almost all values of the studied environmental factors, except for 28°C and 10‰. This means that the transport system of *D. pumila* is equally effective in a wide range of temperature and salinity changes, as well as during extended air exposure and the maintenance of colonies in stagnant water. The highest efficiency of colony integration is achieved at 15–20°C, 26–20‰ and after air exposure for 5–10 min. In terms of the degree of integration, there is almost no difference in the number of colonies in nonflowing and flowing conditions. The transfer of colonies from one cuvette with water to another does not affect the intensity of the hydroplasmic flow system.

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Decentralized modular organisms, e.g., colonial hydroids, demonstrate a high systemic stability as a result of their increased both morphological and functional plasticity. Due to the multiple duplication of various organs (modules), decentralized organisms are resistant to external influences, easily endure damage, and decay into fragments (Marfenin, 2016). Such organisms continue to function effectively and smoothly even under seemingly unfavorable conditions. The tolerance of modular organisms is usually illustrated on the example of their growth, reproduction, and survival in adverse conditions, i.e., long-term processes. However, modular organisms are not communities of individuals but rather a special type of integral decentralized organisms in which there are bodywide systems. In hydroids, this is a general colonial distribution system. It can be expected that its functioning should respond to external influences. To test this assumption, at least two indicators can be used: body pulsations and hydroplasmic movement in the gastrovascular cavity. Both indices make it possible to determine the efficiency of the entire distribution system. An efficient and well-coordinated distribution system is essential for the movement of food from the place of its reception to remote parts of the colony, in particular, to the growing tips and young shoots

(Marfenin, Burykin, 1979; Kosevich, 1991; Dudgeon and Buss 1996; Dudgeon et al., 1999).

The efficiency of the distribution system is expressed in the speed and distance of the transfer of particles suspended in the hydroplasm over the colony for one act of unidirectional continuous hydroplasmic flow, i.e., the formation of fast and extended flows that connect the distant parts of the colony with each other. Extended hydroplasmic flows (HFs), which occur from time to time in a colony of hydroids, are of paramount importance for integration of the organism (Burykin, 2013; Marfenin and Dementyev, 2017, 2019, 2020). They enable the rapid delivery of food particles to growth zones, primarily, to the growth tips of stolons and adjacent areas in which new shoots or hydrants are formed (Kosevich, 1991; Marfenin, 1993; Wagner et al., 1998). The priority provision of food to peripheral growth zones allows colonial hydroids not only to increase in size but also to move along the substrate due to stolon growth; they leave some zones and master others. Therefore, extended HFs play a key role in the life of the colonial organism of hydroids. It is necessary to know the limits of change in the main parameters of the habitat in which the functioning of the HF system remains effective. According to the reaction of the distribution system to changes in the conditions of existence, one can determine the degree

of eurybiontism of the colonial organism, in particular, the degrees of eurythermy and euryhaline, as well as the ability to withstand air exposure. In addition to these problems, we sought to determine the rate of the holistic response of a modular organism to external influences and the ability to maintain an effective mode of functioning outside the preferred values of environmental indicators.

There is reason to believe that the object of study we have chosen is well adapted to extreme deviations of abiotic parameters from the optimum.

The hydroid *Dynamena pumila* (L., 1758) is adapted to life in an unstable littoral biotope and is daily exposed to various abiotic factors. The persistence of hydroplasmic flows after external impact on the colony indicates that the distribution system continues to function even under stress (Dementyev, Marfenin, 2018, 2019a, b; Marfenin, Dementyev, 2018b). But how effectively does it function? In essence, we define efficiency in terms of the capacity of the distribution system for the rapid delivery of food particles from one end of the colony to the other. The greater the particle quantity and distance of movement are, the more efficient is the HF system functioning.

The purpose of the work is to compare the efficiency of the distribution system in the studied range of changes in abiotic environmental factors. We want to determine the degree to which this efficiency varies upon abrupt changes in environmental parameters and, especially, at the extreme values of these parameters beyond which the growth of the colonial organism stops.

The research method we use makes it possible to determine the almost instantaneous reaction of the distribution system to changes in environmental parameters. This reaction can be judged by the nature of the coenosarc pulsations, as well as the speed and distance of hydroplasmic movement in stolons. Reliable changes in these indicators can be determined via microvideo filming for 1 h.

MATERIAL AND METHODS

The object of study is the hydroid *Dynamena pumila* (L., 1758) (Sertulariidae, Leptothecata, Hydrozoa), which has been repeatedly used in various experimental studies of growth, morphogenesis, and ecology. The collection of hydroids, their cultivation, video recording of the functioning of the distribution system, and data processing were carried out according to the previously described method (Marfenin, Dementyev, 2017, 2018a, b, 2020; Dementyev, Marfenin, 2018, 2019a, b).

The hydroid colonies were collected at low water near the White Sea Biological Station (WBS) of Moscow State University on the Yermeevsky threshold of Velikaya Salma in the Kandalaksha Bay of the White Sea. In the laboratory, hydroids were grown on glass

slides in aquariums with circulating sea water at a constant temperature of $15 \pm 1.5^\circ\text{C}$, which approximately corresponding to the sea temperature in the second half of summer. Intensive circulation of water in aquariums was carried out via aeration with micro-compressors through porous atomizers.

Colonies were grown from fragments of individual shoots from the stolon site: the glass was wrapped with thread several times, and a fragment of the shoot was brought under the stretched thread. Its cut plane was oriented toward the glass. In the process of reparative regeneration, the colony at the site of the cut adhered to the glass with chitin secreted at the growth apex, forming a perisarc. Subsequently, the fixing thread was removed. The hydroids were fed to excess daily with freshly hatched nauplii *Artemia salina*. The water in the aquariums was changed every three days.

For recording, the glass with colonies was placed in a nonflow thermostatic cuvette with a displacement of 0.25 L. Video recording was carried out with an Arecont-AV3100 camera through a microscope at a magnification of $\times 100$, and the image was recorded on a computer. The duration of each episode was from 1.5 to 8 h. The time-lapse shooting mode was 4 frames/s. The video recordings, including measurement of the distances of the growth tip from the frame border, the coenosarc lumen, and the particle movement in the hydroplasm, were processed manually.

In the experiments, small, rectilinear colonies with unbranched stolons and large maternal shoots were used (usually 20–30 pairs of hydrants) and small subsidiaries, including one to two pairs of hydrants each (Fig. 1). In this way, each colony consisted of two shoots: a large parent (which could be branched) and one child. There were also two stolon modules, the area between two successive shoots and the area from the youngest shoot to the growth tip of the stolon. The use of extremely short colonies allowed a clearer visualization of the reaction of the distribution system to changes in the values of environmental factors and was limited to the registration of HF coming from a single large shoot.

Time-lapse microvideo was used in the studied colonies to film the *first module* of stolon (between the first, counting from the tip of the stolon, and the maternal shoots). The area between the tip of the stolon and the first shoot from it is called the *zero module*. In it, we did not register the pulsations of the coenosarc or the movement of the hydroplasm. The first module is a formed section of the colony (Marfenin and Dementyev, 2017; Marfenin and Dementyev, 2017).

The method to determine the main parameters and efficiency (speed and distance of movement of particles) of the distribution system is based on long-term registration in one place of only three indices: (1) transverse pulsations of the coenosarc of the stolon; (2) directions and (3) local HF rates.

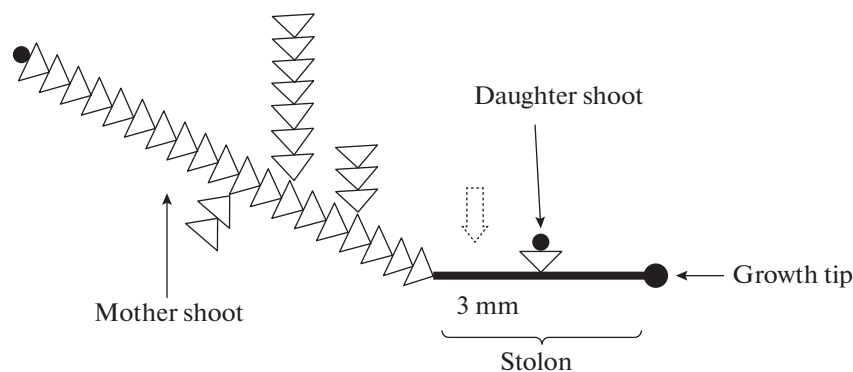


Fig. 1. Generalized scheme of *D. pumila* colonies used in the experiment on the influence of environmental factors. The dotted arrow indicates the place of registration.

The hydroplasmic flow velocity (v_{HF}^- , $\mu\text{m/s}$) was determined as the distance traveled by the recognizable particles in the cavity of the stolon or shoot in 1 s. This indicator (v_{HF}^-) changes constantly: from 0 $\mu\text{m/s}$ to maximum values and then back to 0 $\mu\text{m/s}$. It can be used as an average v_{HF}^- for the comparison of one cycle of HF pulsation and the maximum. We call the latter the amplitude of HF velocity fluctuations (A_{HF}). It is equal to the maximum value of the unidirectional flow velocity.

The cumulative performance indices of the distribution system are (a) the length of particle transfer (Z) for one act of unidirectional local HF and (b) the volume of transferred hydroplasma (V) containing these particles.

The estimated particle-transfer distance (Z , μm) is based on regular determinations of the particle velocity in the hydroplasm (v_{HF}^-). A registration interval of 30 s was chosen. Assuming that the speed is constant within this interval, we multiplied v_{HF}^- for 30 s and obtained the extent of the displaced hydroplasma in 30 s. The values obtained in this way Z were added, and the calculated particle-transfer length for a unidirectional HF from the start to its completion was obtained.

Hence, $Z = \sum_{i=1}^n (v_{HF}^-)_i \times \Delta t$, where i is the serial number of the HF velocity measurement, v_{HF}^- is the HF velocity (length of the particle run in 1 s); and Δt is the registration step (in our case, 30 s).

The Z index represents the sum of continuous runs of particles in one direction with different velocities from zero to the maximum (exponent A_{HF}) and then back to zero. If A_{HF} makes it possible to quantify the intensity of the process of moving particles, according to the maximum v_{HF}^- for one cycle, then Z gives an idea of the range of movement of the HF front, since the front is clearly defined in the HF: it is the boundary

between the particles that have come into longitudinal motion and continue to spin in place.

The hydroplasmic volume (V , μm^3) is the volume of transferred hydroplasma through the cross section of the stolon for an interval corresponding to one HF. It is calculated based on the data on the HF speed (v_{HF}^-), the duration of unidirectional HF, and the size of the stolon coenosarc lumen (D). Assuming conditionally that the HF speed is constant between two successive counts, i.e. for 30 s, we obtain the sum of the values of the volumes of the displaced hydroplasma for each half-minute interval during a unidirectional HF according to the formula $V = \sum_{i=1}^n (\pi D_i^2)/4 \times (v_{HF}^-)_i \times \Delta t$, where i is the serial number of the measurement v_{HF}^- and D ; n is the number of registration steps; and Δt is the registration step (in our case, 30 s).

The transfer length is a more informative index of the efficiency of the distribution system, since even significant volumes of hydroplasm saturated with food turn out to be useless without the possibility of transportation through the colony. They will simply accumulate near the hydrant that has received food.

We call the flows directed toward the apex of the stolon main (+) HF, and those from the apex are compensatory are (−)HF. Accordingly, we distinguish between the indices of an HF moving distally ($A_{(+)HF}$, $Z_{(+)HF}$, $V_{(+)HF}$) and proximally ($A_{(-)HF}$, $Z_{(-)HF}$, $V_{(-)HF}$). The results of this work are based only on the characteristics of the main (+) HF.

When discussing the possibility of particle transfer over long distances, we also use the term “flow length,” but such cases refer to the length of a *generalized HF*, which consists of a set of local HFs. The length of the local HF can be determined numerically based on data on the speed of continuous movement of particles in one direction, which is determined from the results of video recording at one site. The length of generalized HF is determined visually under a binoc-

Table 1. Highest speed or amplitude of HF (A , $\mu\text{m/s}$), length of particle movement (Z , μm) and HF volume (V , μm^3) in the first *D. pumila* stolon module. For comparison, the increase in the stolon apex per one pulsation is indicated (m_{gp} , μm)

Environ- mental factor	Factor value	Distribution system index						m_{gp}	
		$A_{(+)HF}$		$Z_{(+)HF}$		$V_{(+)HF}$			
		$\bar{x} \pm SE$	n	$\bar{x} \pm SE$	n	$\bar{x} \pm SE$	n	$\bar{x} \pm SE$	n
Tempera- ture	10°C	25.1 ± 2.4	33	2192 ± 273	40	5505885 ± 910439	40	14.0 ± 0.8	51
	15°C	41.1 ± 4.5	45	3101 ± 255	50	7764190±1093795	50	15.3 ± 1.1	52
	20°C	37.3 ± 4.2	61	2232 ± 248	67	4500050 ± 667303	68	15.4 ± 1.0	79
	25°C	27.4 ± 2.3	82	1560 ± 134	90	3462456 ± 483495	89	7.2 ± 1.8	105
	28°C	17.0 ± 1.4	70	1018 ± 95	74	1038013 ± 192082	74	1.6 ± 0.8	49
Salinity	26‰	33.8 ± 2.9	55	2919 ± 300	61	4170077 ± 563206	59	12.7 ± 1.1	43
	20‰	38.9 ± 4.3	55	2656 ± 252	67	5584866 ± 749314	67	15.4 ± 1.2	42
	15‰	30.5 ± 2.1	57	2298 ± 153	64	4082916 ± 385662	63	4.9 ± 0.7	161
	10‰	23.1 ± 4.2	31	2257 ± 358	34	2935789 ± 496458	34	0.7 ± 0.7	9
Dehumid- ification	Without dehu- midification	23.3 ± 1.6	66	1994 ± 152	79	3888090 ± 413221	76	12.1 ± 1.0	56
	For 5 min	29.5 ± 3.1	35	2608 ± 284	39	4011455 ± 501344	38	11.8 ± 0.9	36
	For 10 min	29.4 ± 2.7	27	2612 ± 258	41	4139642 ± 583980	41	13.8 ± 0.9	69
	For 20 min	26.4 ± 2.0	53	1782 ± 176	68	2665393 ± 355461	68	7.4 ± 0.8	38
	For 30 min	30.5 ± 1.7	146	2208 ± 121	179	3383962 ± 275239	178	3.7 ± 0.7	121
Water exchange	In still water	40.5 ± 2.7	73	2218 ± 152	79	6544997 ± 537849	78	14.4 ± 2.7	129
	In running water	33.5 ± 2.2	51	2056 ± 153	77	5028507 ± 396721	76	8.0 ± 3.1	119

ular at low magnification via movement of the cuvette with the colony (Marfenin, Dementyev, 2019).

The study uses previously published data on the impact of environmental conditions on *D. pumila*. The novelties in this article are: first, a comparison of the response of the colony's distribution system to the impact of various environmental factors and, second, an analysis of the efficiency of the distribution system's functioning in the case of deviations from the optimal values of indices of the state of the environment.

The response of the distribution system to four abiotic environmental factors was studied in the following ranges:

- temperature (10, 15, 20, 25, 28°C);
- desalination (26, 20, 15, 10‰);
- air exposure (duration 5, 10, 20, 30 min);
- the absence or presence of water exchange in the cuvette.

For control values, we take the average salinity of water at the place of material collection (26‰), the material cultivation temperature (15°C), the lack of air exposure, and the presence of water exchange.

A total of 29 different *D. pumila* colonies were examined: six in the experiment with temperature, six in the experiment with salinity, eight in the experiment

with drying, and nine in the experiment with water exchange. We did not attempt to study the adaptation of colonies to a gradual change in conditions (e.g., heating or desalination) and studied only the short-term, primary reaction to a change in the value of the environmental factor.

The statistical characteristics of the results presented in the work (arithmetic mean \bar{x} , standard error of the mean $\pm SE$, sample n) for the length and volume of HFs in the first module of the *D. pumila* stolon were calculated in the Excel program for all episodes filmed together under the same conditions (e.g., at the same salinity value) within the experiment. These data were obtained and published by us earlier (Dementyev, Marfenin, 2018, 2019a, b; Marfenin, Dementyev, 2018b). The summarized data are presented in Table 1. Although the experiments were carried out in different years and on different *D. pumila* colonies, it is quite acceptable to compare the data of different articles, since we used the same cultivation conditions, registration technique (remote), and methods of data processing and quantitative analysis. The nonparametric Mann–Whitney test was used to assess the reliability of the obtained values.

In the course of the study, it was found that the average HF lengths are insufficient to understand the formation of the main flows passing along the stolon

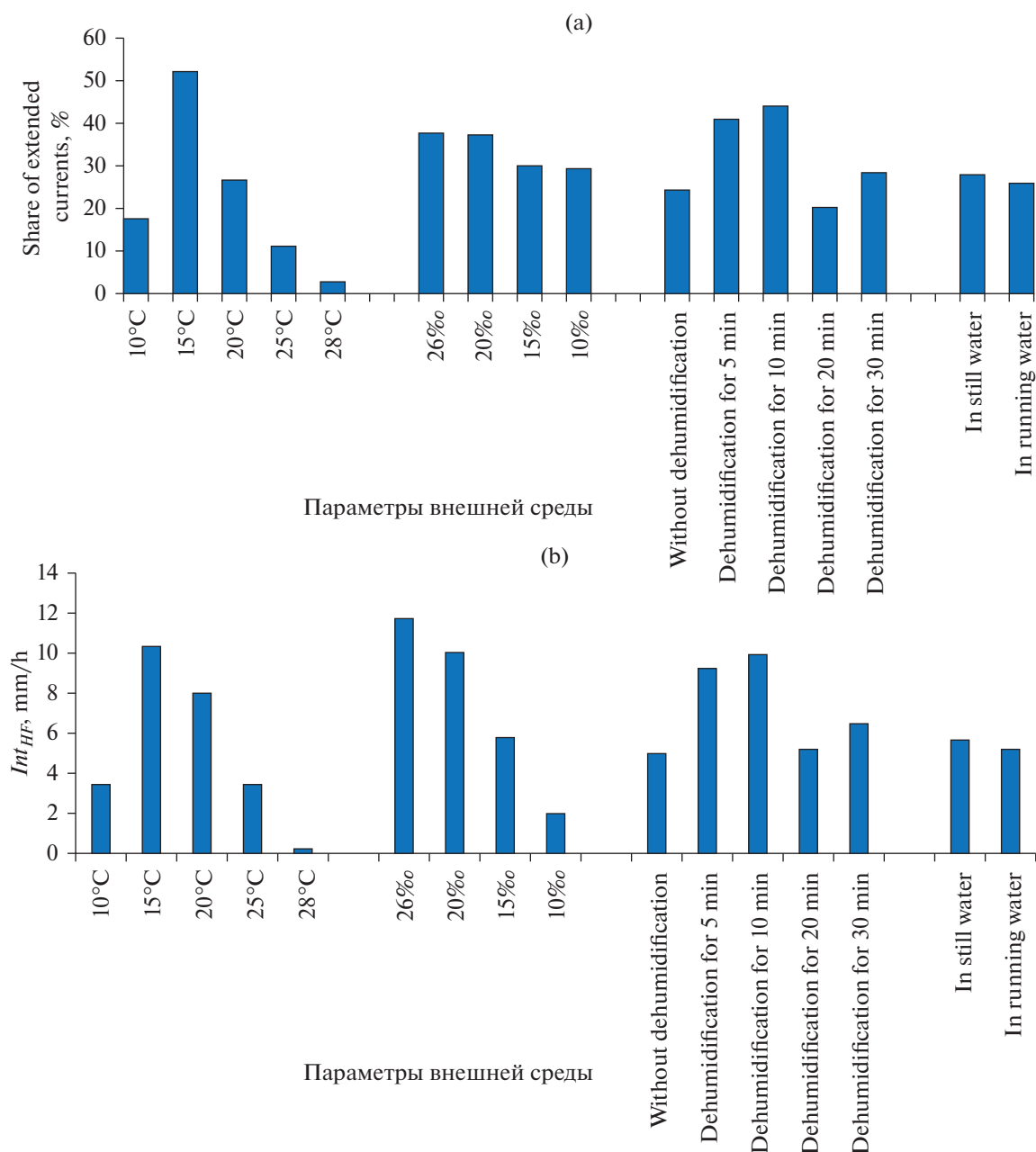


Fig. 2. Proportion of extended (more than 3 mm) flows (a) and integration-efficiency index int_{HF} (b) in the first *D. pumila* stolon module under the studied environmental conditions.

through the entire colony. Therefore, extended (more than 3 mm) (Fig. 2) and “volume” (more than 4800000 and $9600000 \mu\text{m}^3$) (Fig. 3) flows were distinguished within the HFs in order to determine their share of the total number of HFs taken into account in the experiment. In addition, to compare all the experiments, we subdivided the HF by length into three groups: less than 2, 2–6, and 6–17 mm (Fig. 4).

To compare the response of the distribution system to the conditions of colony maintenance, the average values of the stolon growth index for one cycle of growth pulsations are also given (m_{gp}). The growth pul-

sations of the stolon apex were determined from the results of video recording under the same conditions in the same colonies as for HF. The details of the method were described earlier (Dementyev and Marfenin, 2018, 2019a, b; Marfenin and Dementyev, 2018b). Shooting of the growth apex of the stolon took place no later than 1.5 h after the shooting of HF.

To determine the efficiency of the distribution system, we were guided by a previously published model of its functioning (Marfenin, 1985, 1993; Marfenin, Dementyev, 2017).

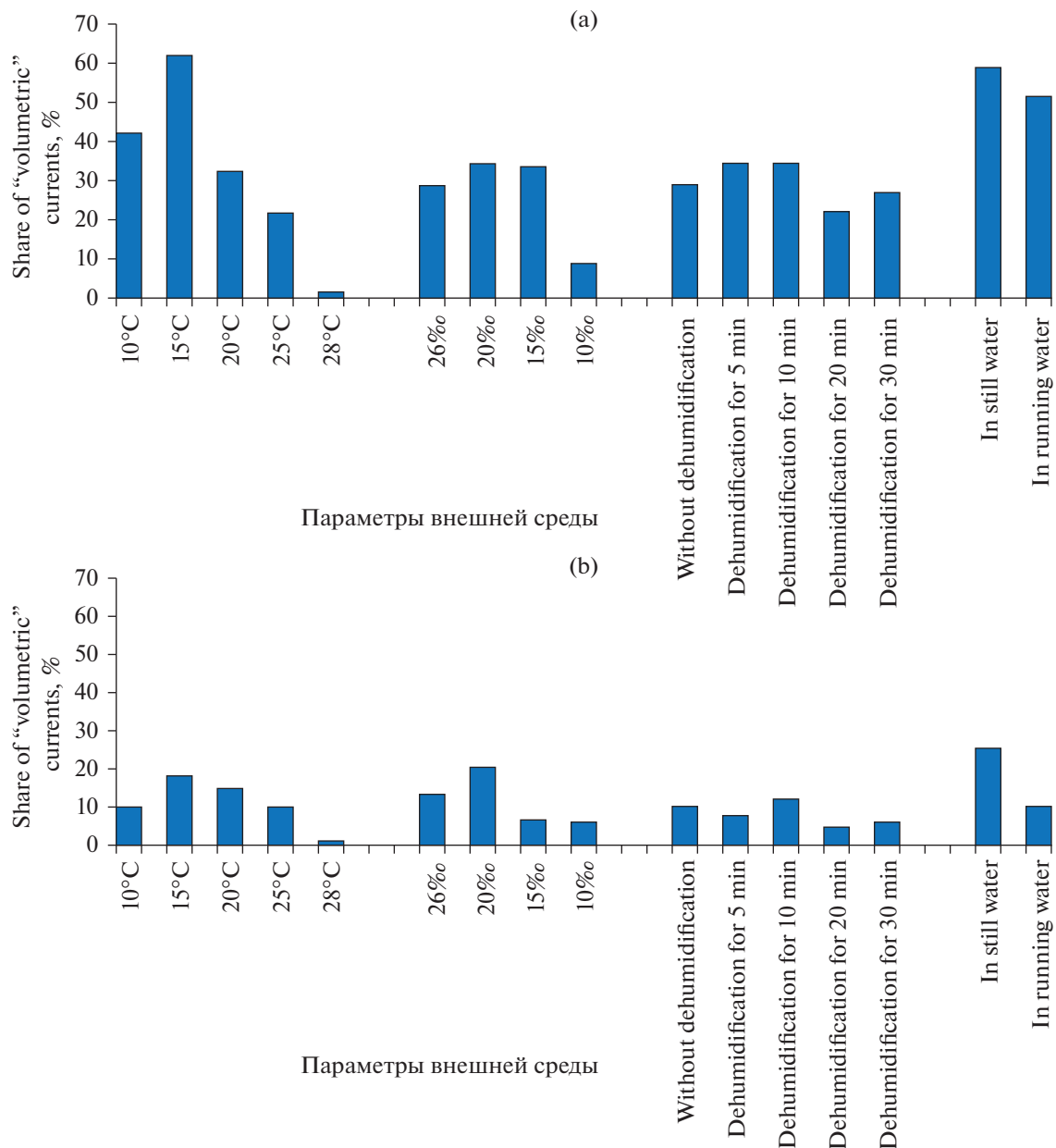


Fig. 3. Proportion of flows with a volume of more than 4800000 (a) and 9600000 (b) μm^3 entering the first *D. pumila* stolon module under the studied environmental conditions.

The movement of particles through the entire colony is possible with the successive connection of intermediate shoots, each of which helps to push the hydroplasm column when it is in close proximity to the shoot. In order for each subsequent shoot to "work," a portion of the hydroplasma must pass through the stolon section that separates this shoot from the previous one. If the HF length Z is greater than the length of one stolon modulus, then long-range particle transport is possible. If Z is less than one stolon modulus, then long-range transfer is theoretically impossible: the particles will move back and forth between two shoots within one stolon modulus. The

length of the *D. pumila* stolon module can vary from 1.5 to 6 mm, but the average length of the formed module is 2.98 ± 0.12 mm; about 3 mm (Marfenin and Dementyev, 2017). The still unformed zero module of the stolon is always shorter. This model provides an acceptable explanation for the mechanism of hydroplasmic movement in short colonies consisting of only two stolon modules. When the HF is greater than the length of one stolon module, it can reach the apex of the stolon growth without the participation of an intermediate young shoot. However, this option is rather an exception to the general rule, according to which part of the hydroplasm, when moving from the

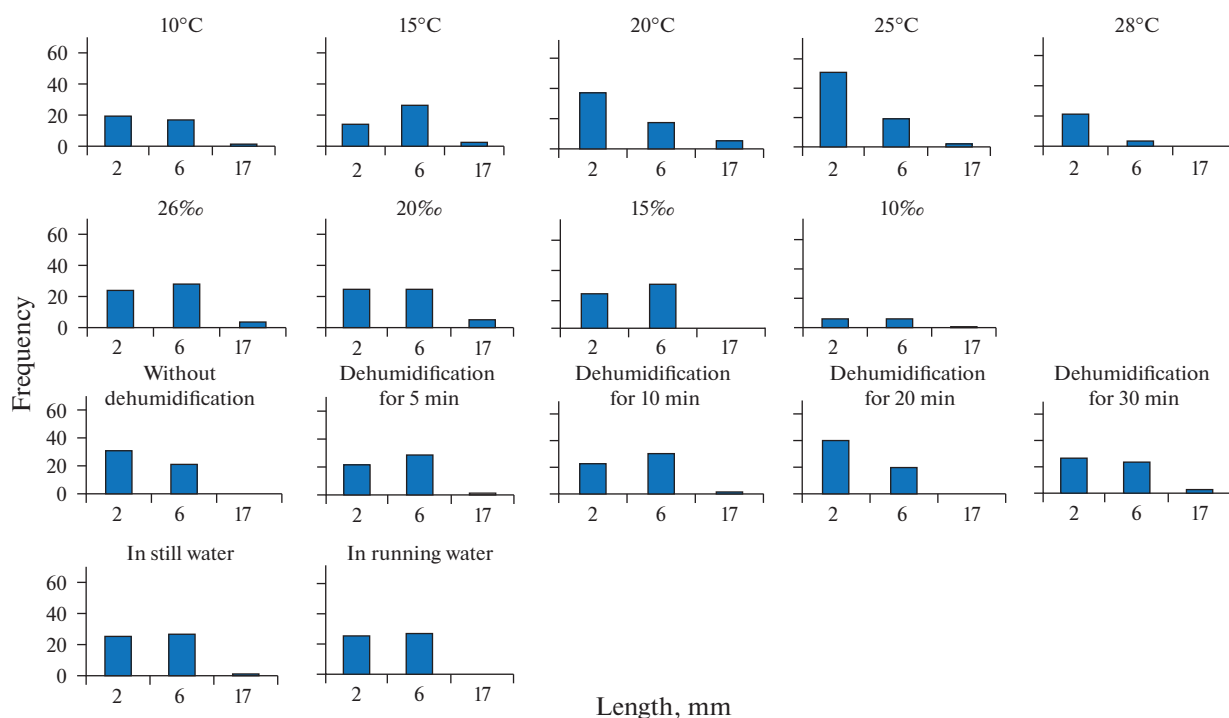


Fig. 4. Interval variation series of HF lengths in *D. pumila* stolons under the studied environmental conditions. Designations: frequency, number of HFs with a given length in 10 h; length “2,” less than 2 mm (length less than the length of one module), “6,” 2–6 mm (one or two modules), “17,” 6–17 mm (more than two stolon modules).

maternal shoot to the tip of the stolon, will still enter the young shoot.

Based on the model described above, the HF volume can be determined. *In fact, the HF volume (V_{HF}) is the product of the extent (i.e. length) of the flow Z on the cross-sectional area of the coenosarc through which this current passes.* Since the size of the coenosarc lumen changes due to lateral pulsations, this should be taken into account in the determination of the average value of its cross-sectional area. The intensity of the lateral pulsations of the coenosarc decreases with distance from the growth apex. Lateral pulsations of the coenosarc in the second and subsequent modules of the stolon are much weaker than those in the first and especially zero modules (Marfenin and Dementyev, 2017). We previously have established on the example of larger *D. pumila* colonies that the diameter of the coenosarc lumen (D) in the first and subsequent modules of the stolon is on average about 45 μm (Marfenin and Dementyev, 2017). The cross-sectional area of the coenosarc ($(\pi D^2)/4$) in this case is equal to 1590 μm^2 . The distribution system is efficient if the length of the local HF covers the distance between adjacent shoots (3 mm or 3000 μm) in the *D. pumila* colony. Multiplying the length of the “efficient” flow by the cross-sectional area of the stolon’s coenosarc, we obtain the volume of the “effective” HF: 4 800 000 μm^3 . In a similar way, one can calcu-

late the HF volume (9600000 μm^3) passing through two stolon modules (6 mm or 6000 μm).

Based on quantitative data (Table 1), we calculated the fractions of extended (more than 3 mm) and volumetric (more than 4800000 μm^3 and 9600000 μm^3) flows in the total number of flows.

We also constructed interval variational series of the frequency of the occurrence of HFs of various lengths in *D. pumila* stolons at the studied values of environmental factors. To do this, we grouped the quantitative values of the length into three options. The choice of variant is determined by the average length of the *D. pumila* stolon module (3 mm): (1) less than 2 mm (length less than the length of one module); (2) 2–6 mm (one–two modules); (3) 6–17 mm (more than the length of two modules)¹.

Since the duration of the video recording episodes varied significantly (from 1.5 to 8 h), combination of the samples for each episode within a specific environmental factor created a significant scatter in time (from 10 to 30 h). In this case, the use of all options was inappropriate: longer episodes would show a significant superiority in the number of registered flows. To eliminate such a statistical error in the incidence of HF, all environmental parameters were recalculated for a constant time interval of 10 h.

¹ The maximum duration of the HF recorded in this study is 17 mm.

To assess the efficiency of the distribution system, we introduced a special index for the first time.

The integration efficiency index (int_{HF}) is the product of the average length of HFs exceeding a given limit (3 mm is the length of the stolon modulus) by the number of such HF per hour (i.e., the frequency of extended HF).

The method described above was used by us earlier to study the reaction of the same type (*D. pumila*) on changes in the temperature, salinity, water exchange and air exposure. The results of the studies were published at different times as the experiments were completed and the results were processed for each of the above habitat parameters, but they were not merged. Only now can we answer a more general question: how typical is it for *D. pumila* to maintain the efficiency of the distribution system in the face of sudden changes in various environment settings.

RESULTS

The estimated length of particle transfer (indicator Z) in the first module of the stolon in colonies varies, but, in general, the environmental conditions in the studied range have little effect on the HF length. Within the same range of changes in environmental parameters, other vital indicators, e.g., an increase in stolon per cycle of growth pulsations (m_{gp}), react more actively, changing by two to three times (Table 1).

At the control values of environmental parameters (26‰, 15°C), which are close to natural in the habitats of the species in summer, the indicator Z in a stolon is approximately equal to 3 mm, i.e., the distance between adjacent shoots (Table 1). The longest HFs are 10.6 mm towards the tip of the stolon and 12.8 mm from the tip to the maternal shoot (at 26‰). The length of the displaced hydroplasm in the first module of the stolon at different salinities does not differ significantly ($p > 0.05$) (Table 1) and is resistant to desalination. Even at 10‰ the average value $Z_{(+HF)}$, i.e., HFs directed towards the stolon apex, is still quite large, and the proportion of extended $Z_{(+HF)}$ is almost 30% (Fig. 2a). The average highest speed per pulse cycle, i.e., HF amplitude (A), in the first stolon module shows a weak and unreliable trend ($p > 0.05$) toward a decrease with desalination (Table 1).

In stolons, Z decreases significantly ($p < 0.01$) at temperatures above 15°C (Table 1). Although the average calculated length of particle movement to the tip of the stolon $Z_{(+HF)}$ at 10 and 20°C is less than 3 mm, the operation of the distribution system should not be disturbed, since the proportion of individual flows with a greater extent is large (Fig. 2a), i.e., not all flows reach the tip—only the most powerful of them do. The longest HFs are 8.9 mm towards the stolon apex (at 15°C) and 16.6 mm from the tip to the mother shoot (at 20°C). Upon further heating to 25 and 28°C, Z decreases to 1–1.5 mm, which covers only half the

length of the stolon module. At the same time, the share of individual extended HF turns out to be insignificant, no more than 10%. These temperature indicators turn out to be a threshold; when they are exceeded, the hydroplasm movement becomes inefficient for particle transport to the growth tips of the stolon and the young shoot closest to it.

In the first stolon module, the amplitude of the HF apex directed ($A_{(+HF)}$) reaches a maximum at 15°C and decreases with further heating of the water.

The flow length (Table 1) in the studied range depends weakly on the duration of air exposure. The amplitude of the HF increases with an increase in the duration of drying (Table 1); however, there are significant differences only between the extreme variants of the experiment (control and 30-min drying). The amplitude of the main flows directed toward the tip of the stolon $A_{(+HF)}$ is higher in still water than in running water. In stagnant and running water (Table 1), the particle-transfer length is 2–2.5 mm.

The share of extended flows (more than 3 mm) usually amounts to 10–40% of the total number of HF (Fig. 2a), but it can be lower (at 28°C) or higher (at 15°C).

Calculation of the integration efficiency index (int_{HF}) of the colony through the work of the distribution system found the following results with respect to environmental indices (Fig. 2b):

- the optimum temperature for colony integration is 15°C;
- desalination leads to a linear decrease in effective integration;
- after a short air exposure, integration increases;
- in stagnant and flowing water, the integration of unidirectional flows is the same.

The change in volume $V_{(+HF)}$, as well as the change in lengths in the corresponding experiment (heating, desalination, drying), generally shows the same dynamics (Table 1, Fig. 3). These volumes make it possible to predict the volume of hydroplasma that should enter the first stolon module (where video recording was performed) for efficient particle transport through the colony. The volumetric HFs account for a significant proportion (sometimes up to 30–40%) of the total number of flows in the studied range of environmental factors (Fig. 3a), although HFs of more than $9\,600\,000\,\mu\text{m}^3$ (i.e., more than 6 mm) are less common (Fig. 3b). An exception is the temperature of 28°C, at which there are very few or no volumetric extended HF. Thus, intense, extended HFs (more than one stolon modulus) exist in the colony; they are not isolated, and the long-range transport of particles is based on them.

Let us consider the interval variational series of HF length in *D. pumila* stolons at the studied values of environmental factors (Fig. 4), which mutually complement the calculation results int_{HF} .

With an increase temperature from 10 to 25°C, the frequency of HFs with a length of more than 2 mm changes insignificantly, although the frequency of short HFs (less than 2 mm) increases by two to three times at 20 and 25°C. At a temperature of 28°C, the frequency of short HFs decreases, and long HFs become rare (Fig. 4).

Upon desalination from 26 to 15‰, there are no significant changes in the frequency of short and extended HFs; the distribution system is well adapted to desalination and continues to function fully (at least in short model colonies). At 10‰, the frequency of all HFs, both short and extended, decreases by almost two times. Consequently, the efficiency of the distribution system at 10‰ significantly decreases (Fig. 4).

Drying up to 30 min inclusive has practically no effect on the HF frequency. The water-exchange parameter (still or running water) does not affect the efficiency of the distribution system for both short (less than 2 mm) or longer flows (Fig. 4).

The average values of stolon growth per one act of growth pulsations (m_{gp}), which were registered at about the same time as the HF, are more sensitive to the conditions of detention. A significant reduction m_{gp} occurs already at 25°C, as well as at 15‰ and after drying for 20 min. At 28°C or at 10‰, the stolon growth almost stops, only a few hours after the transfer of colonies to such conditions (Table 1).

DISCUSSION

A comparative study of the reaction of the distribution system of colonial hydroids to external influences was carried out for the first time. In the past, more attention was paid to the growth and branching of the colony as indices of the impact on the colonial organism (Burykin, 1978a, b, 1979) or population indicators for noncolonial hydroids (Kanaev, 1952). Changes in growth and branching are slowly detected with existing methods, after a day or more (Marfenin, Burykin, 1979). They reflect a significant restructuring of the entire colonial organism. This restructuring does not become noticeable immediately, but it lasts a long time, sometimes for a week or more, which is a significant period in the life of colonial hydroids.

The faster reaction of hydroids to external influences is expressed by the pulsation of the coenosarc and in the behavior of hydrants. When any adverse circumstances occur, the hydrants are compressed. Thus, they react to air exposure, a sharp change in temperature, water flows, etc. Pulsations of the coenosarc are also sensitive to external influences, especially pulsations of the growth tips (Dementyev, Marfenin, 2018, 2019a, b; Marfenin, Dementyev, 2018b). However, both the behavior of hydrants and the pulsations of the coenosarc largely reflect local circumstances. It is impossible to use them to judge the effect of influences on the whole organism as a whole.

The efficiency of the functioning of the distribution system, which is expressed by the speed and volume of particles carried by the hydroplasma, is the basic index of the vital activity of the colonial organism; it is the same as growth and branching, but it is determined much faster (in a few hours). Rapid methods described in the literature for the study of HFs, such as the introducing a radioactive label (Rees et al., 1970) or fluorescent dyes (Makarenkova, 1988; Buss et al., 2015) into food, require special equipment. In addition, these methods are not sufficiently useful, since they only make it possible to determine the general direction, distance, and duration of the movement of marks; it does not specify the process of HF formation, its dependence on the local HF components, or the dynamics of the functioning of the distribution system.

Video recording of the hydroplasma movement in stolons in colonial hydroids makes it possible to identify, simply and without contact, the reaction of the distribution system to various influences affecting the colonial organism. The delay period of the reaction to the impact corresponds to one or two HF cycles, i.e., 30 min to 1 h. In fact, this is an instantaneous reaction of the body, since all processes in colonial hydroids, except for the behavior of hydrants, occur slowly, over tens of minutes.

Using the key role of the distribution system in the life of hydroids and the ability to quickly register its response to external influences, we can approach the solution of a number of problems, both fundamental and applied. The fundamental problem is to determine the degree of tolerance of a modular organism, the ability to survive unfavorable periods, and the insensitivity to stressful influences.

The applied problem is to determine the duration of the permissible change in environmental conditions under which the colonial organism does not react by restructuring its vital processes to short-term air exposure, changes in temperature or salinity, maintenance in still water, etc.

In this regard, we consider two questions: (1) how the HF system reacts to sudden changes in environmental conditions; and (2) whether the system remains effective.

Analysis of the indicators of the hydroplasma movement made it possible to identify the ecological limits of normal *D. pumila* existence on several parameters. Normal existence refers to the preservation of efficient transportation of intracavitary fluid throughout the colony, i.e., the ability to deliver particles from the largest shoot to the zero modulus closest to the growth tip of the stolon.

The capacity for the extended transport of food particles in the stolon of a colonial hydroid is generally determined by the calculated length of the local HF recorded during microvideo filming. As shown earlier (Marfenin and Dementyev, 2017), local HFs form

continuous unidirectional integral HFs. They spread over considerable distances; the maximum is the length of the entire stolon: from its proximal end, where the largest (maternal) shoot is located and from which the model colony was grown, to the growth tip of the stolon at its distal end (Marfenin and Dementyev, 2019).

If the calculated length of the local HF is greater than the average length of the stolon module, then there are conditions for the successive participation of shoots along the stolon in the hydroplasm movement inside it. According to this hypothesis, the local HF partially enters the nearest shoot, causing an expulsion of excess hydroplasm from it, i.e., generating the next local HF, and so on (Marfenin, 1985).

If the calculated length of the local HF is less than the average length of the stolon module, then there are no necessary conditions for the formation of a unidirectional extended HF. Such a flow means that there is only a slight shift of the hydroplasm in the stolon within one module, followed by its “rollback.” At the same time, the food particles remain within one module of the stolon. Therefore, the HF system becomes inefficient when the length of local HF is less than the average length of the stolon module. If the same HF system has average local HF lengths greater than the length of the stolon modulus, it is recognized by us as efficient, i.e., sufficient for the formation of continuous extended flows.

Between the two states of the HF system defined above, effective and inefficient, there may be intermediate states. In the comparison of the average lengths of the stolon modulus and the calculated length of the local HF, it should be remembered that averaging brings together all of the variety of averaged values. These include both short and long modules (Marfenin and Dementyev, 2017), as well as short and long local HFs.

The standard error of the mean gives some idea of the real variety of averaged values, but not completely. Somewhat more information can be obtained by if the proportion of extended HF (more than 3 mm) in the total number of flows in the first module of the stolon is taken into account. This index turns out to be significant for all tested values of abiotic factors (Fig. 2).

We received most of the information from the variational series demonstrating the relationship between the averaged values (Fig. 4); in our case, this is the ratio of the lengths of local HF, which is divided into three groups:

- the first group (up to 2 mm) has flows insufficient to generate extended HF;
- the second group (from 2 to 6 mm) has a local HF of medium length that covers one or two stolon modules and is theoretically sufficient to generate a chain of local HF constituting a jointly extended HF;
- the third group (from 6 to 17 mm) has flows that spread over two or more stolon modules.

The comparison results presented in Fig. 4 convincingly indicate that the main condition for the generation of extended HFs, the flows of the second group, are equally represented for almost all values of the studied environmental factors, except for 28°C and 10‰.

Therefore, even in those cases where the average value of local HFs is less than the average length of the stolon modulus, there may be separate local HFs sufficient to overcome the distance between adjacent shoots. In these cases, integral HFs that carry food particles over a considerable distance along the stolon form. Since such integral HFs occur irregularly, the efficiency of the HF system is obviously lower as compared to those cases in which the average values of local HF are higher than the average values of the stolon modulus length.

When stating the inefficiency of the HF system, one should still pay attention to the value of the standard error $\pm SE$ (Table 1) and the results of data analysis with variational series (Fig. 4). The larger the value of the standard error is, the more likely it is that the HF system, even with an insufficient average value of the estimated length of the local HF, from time to time generates flows capable of providing an extended “relay”² transmission of particles over a considerable distance along the stolon.

Obviously, the integration of a colony is determined not only by extended HFs but also by their frequency. The higher is the proportion of extended HFs exceeding the average length of one stolon module (3 mm), the more efficient is the supply of food to the distally located growth zones. To account for both of the components, we introduced the integration-efficiency index int_{HF} , which is the total length of all extended HFs per hour (Fig. 2b). The comparison in Fig. 2 of the pairwise course of similar diagrams shows that they almost coincide for experiments with temperature, drying and hydrodynamics, while they differ significantly in the experiment with salinity. This means that, as desalination progresses, the average HF length exceeding 3 mm decreases. Therefore, the integration efficiency index int_{HF} is more informative than the index of the frequency of extended HFs, and it can be recommended for the analysis of physiological integration in colonial hydroids.

Following this recommendation, it is possible to take into account the intermediate states of the efficiency of the distribution system, not only the two extreme options of efficient and inefficient HPF systems. In this case, the presented results (Fig. 2b) allow us to consider that the distribution system is most efficient at 15 and 20°C, 26 and 20‰, and with drying for 5 and 10 min. With the number of colonies in stagnant

² The term “relay” transmission of particles was proposed by Yu.B. Burykin (2013).

water, the efficiency is the same as in the presence of water exchange.

In the analysis of the HF length and the volume of hydroplasm carried by flows, it should be remembered that all experiments were carried out on extremely short colonies consisting of one large (maternal) shoot and one small (daughter) shoot. The stolon length in these colonies was 5–6 mm. It is all the more surprising that the estimated length of HFs emanating from the maternal shoot is on average 2–3 mm and the maximum is 10.6 mm, even in such tiny colonies. How is this possible? The volume of the zero module of the stolon, the area behind the growth apex, is significantly larger than the volume of any other stolon module. It is equivalent to three to five stolon modules between shoots (Marfenin and Dementyev, 2017). Also, the shoot apex, or rather, the section of the stolon below it, is much larger than the shoot coenosarc module and the stolon module (our unpublished data). Together, this complex (the zero module of the stolon and the nearest young shoot) can receive significant volumes of hydroplasm released from the mother shoot. The maximum values of the calculated volume of one HF established by us exactly correspond to the maximum values of the volume of the zero module of the stolon.

Similar experiments were not carried out on long colonies. In large colonies, the perisarc of the part of the stolon removed from the apex becomes dark, which prevents the registration of HF via microvideo filming. However, direct visual tracking of the particle movement in a stolon under a binocular showed that these particles can move without interruption from one end of a colony consisting of eight stolon modules (seven formed and a growing zero one) to its opposite end (Marfenin, Dementyev, 2019).

The study of the impact of environmental factors on the colonial organism of a hydroid *D. pumila* showed that coenosarc pulsations and indices of hydroplasmic movement often varied significantly (Dementyev, Marfenin, 2018, 2019a, b; Marfenin, Dementyev, 2018b), including cases in which the values of abiotic factors were close to natural for the colony. The noted variability of the data may be the result of the constant processes of self-regulation in a modular organism (Marfenin, 2016). This important circumstance should be taken into account in the analysis of the reaction of the distribution system to external influences. In the comparison of an HF system under changed conditions of existence, it is necessary to take into account the fact that the HF speed, their periodicity, and their range vary significantly, even under constant conditions. This is a characteristic feature of decentralized organisms (Marfenin, 2016).

We based this comparative analysis on the primary results of previous partial studies of the reaction of *D. pumila* to heating, desalination, air exposure, and changes in water exchange (Table 1). The characteris-

tic variability of HF indicators is smoothed out by the presence of the trends described by us earlier (Dementyev, Marfenin, 2018, 2019a, b; Marfenin, Dementyev, 2018b).

The optimal range in which intensive hydroplasma movement and large volumes of transferred hydroplasma are recorded is from 10 to 20°C and from 26 to 15‰. Upon further heating (25 and 28°C) and desalination (10‰), the hydroplasmic movement loses its activity, becoming slower, less extended, and less voluminous (Table 1). Air exposure for a short period (up to 30 min inclusive) does not clearly affect the operation of the distribution system, although it leads to a slowdown in stolon growth (Dementyev and Marfenin, 2019a). In a still-water distribution system, *D. pumila* functions more vigorously: with a higher frequency of the occurrence of powerful HFs, their greater speed, and greater volumes of transferred hydroplasma (Marfenin and Dementyev, 2018b).

Only when the temperature reaches 25–28°C is there a decrease in the efficiency of the distribution-system functioning, but extended HFs do not disappear completely even at such a high temperature for a hydroid (although they become rare). In other cases, the distribution system remains efficient, i.e., it is able to ensure particle transfer to the growth zones, despite a decrease in growth and even a halt in the growth of the colony (Dementyev and Marfenin, 2018, 2019a, b).

The HF indices react “softly” to changing environmental conditions. With a stepwise change in temperature and salinity, a gradual increase in the duration of drying, and the absence of water exchange, it would be expected to see a linear response (e.g., a smooth decrease in all indices). However, this does not happen (Fig. 4), except for the experiment with desalination (Fig. 2b). The change in the nature of HFs with each new impact on an individual colony in the studied range of environmental factors is almost imperceptible. Based on the analysis of HFs, we cannot establish that the system has sensed a change in environmental conditions at this particular moment. The reaction immediately after the parameter change is not noticeable. Current indices do not change quickly or by much (Dementyev, Marfenin, 2018, 2019a, b; Marfenin, Dementyev, 2018b). Only with the averaging of a lot of data over many colonies can some trends can be distinguished, but, even then, they are not quite distinct.

Near extreme values of HF environmental parameters continue (Fig. 4), although other physiological indicators are violated. Growth declines until it stops (m_{gp} in Table 1); moreover, the period and amplitude of the growth and lateral pulsations of the body change (Dementyev, Marfenin, 2018, 2019a, b; Marfenin, Dementyev, 2018b).

The persistence of HFs indicates that the distribution system continues to function, even under stress.

As characteristic organisms that live on the border of the lower littoral and sublittoral, the hydroid colonies studied by us, *D. pumila*, are exposed to strong abiotic influences. Until now, it has remained completely unclear whether abiotic stress causes any disturbances in the functioning of the distributive system and, if it does, the degree of their severity. Analysis of the parameters of the distribution-system functioning made it possible to show the degree of HF stability under external influences (temperature, salinity, etc.) that are close to natural in the habitats of the species in summer.

This confirms the lability of the decentralized distribution system. In the modular organization inherent in hydroids, noncentralized regulations become possible. This enables a higher stability of the system due to the development of the plasticity of physiological processes. Hydroids are able to adapt to the characteristics of their habitat due to their “natural” variability (Marfenin, 2002, 2016). The relatively simple structure of the hydroid organism demonstrates plasticity of the response to external influences: completely different environmental factors in the studied range cannot destabilize the system. The physiological process of food transfer through the colonial organism is not significantly disturbed even if the conditions deviate from the optimal ones for the hydroid. Though *D. pumila* and is a littoral form that lives in unstable conditions of the tidal band, it is still possible to identify the most optimal indicators of abiotic factors for it. The values of environmental factors used in the experiments (10–28°C, 10–26‰) correspond to the temperature and salinity regimes in the littoral of the White Sea coast in summer (Naumov and Olenov, 1981; Tsetlin et al., 2010). However, the optimal range for a high growth rate, intensive hydroplasmic movement, and the largest volume of transferred hydroplasma is from 10 to 20°C. The hydroid *D. pumila* can exist without signs of oppression in the salinity range from 26 to 20‰ for at least 8 h (Dementyev, Marfenin, 2018, 2019a, b). Colonies withstand drying up to 30 min inclusive: growth slows, but there are no significant changes in body pulsations or hydroplasmic movement even after 7–9 h of observations.

The established tolerance of the *D. pumila* distribution system to abiotic influences is of practical importance. It allows the use of the following procedures in experimental work with hydroids: (1) the transfer of glasses with colonies from one cuvette to another; (2) manipulations with hydroids in a nonflowing cuvette with stagnant water; (3) the feeding of hydroids in a separate aquarium at a temperature different from the cultivation temperature; (4) a forced content in water with different salinities (taken from the sea and not standardized), etc. The obtained data make it possible to remove many questions about the admissibility of certain procedures in laboratory studies of hydroids, which are important model objects (at least for the frequently used type *D. pumila*).

We examined the efficiency of colony integration not only in terms of its presence or absence but also using the criterion of the frequency of the integration of extended HFs. The formation of local flows sufficient for efficient hydroplasm movement over the colony is possible under all studied environmental conditions, although with different frequencies. The studied parameters of the medium do not lead to a complete cessation of hydroplasma transport through the colony (even at 10‰, HFs remain in the stolons, and there are flows with a length of more than 3 mm at 28°C). The distribution system remains theoretically efficient for any temperature, salinity, drying time, and water exchange tested. The established stability of the distribution system (during the first hours of exposure to the factor) is proof of the tolerance of the hydroid to the deviation of the environmental parameters from the optimal values for the organism. Apparently, tolerance is a characteristic feature of the distribution system of the littoral hydroid *D. pumila*.

CONCLUSIONS

Comparison of the results of studies of the reaction of the hydroid *D. pumila* to changes in environmental conditions showed that the distribution system of this type reacts poorly in the first hours of a sharp deviation from the optimum in several main environmental factors: temperature, salinity, air exposure, and water exchange.

The distribution system of *D. pumila* remains theoretically effective in a temperature range of 10–28°C, a desalination range of 26–10‰, dehumidification for up to 30 min, and a lack of water exchange. However, the optimal conditions for the functioning of the HF system are 15–20°C, 26–20‰, and short-term drying for 5–10 min. Differences in the efficiency of the functioning of the distribution system with respect to the number of colonies in stagnant water and the course have not been established.

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