hydrobiology

MDPI

Article

How Tolerant Are Hydroids to Climate-Change-Induced Acute Spikes in Sea Water Temperature? A Case Study of Arctic *Dynamena pumila* (L., 1758)

Nikolay N. Marfenin *, Vitaly S. Dementyev and Evgeny V. Nikolaev

Department of Invertebrate Zoology, Lomonosov Moscow State University, 119234 Moscow, Russia
* Correspondence: marf47@mail.ru

Abstract: The temperature of the water surface layer in the Arctic may increase significantly in the coming decades. To what extent will shallow-water fauna be affected by warming? We investigated this issue using an example of one species of colonial hydroid, *Dynamena pumila*. We judged its reaction to warming via its pulsation activity and the growth of stolons. Pulsations of the coenosarc in colonial hydroids are a sensitive indicator of the body's reaction to the influence of environmental factors. We tested the ability of *D. pumila* colonies to survive and adapt to existing at 25 °C for five days. After raising the temperature from 14 °C to 25 °C, colony growth and the pulsation of stolon growth tips on the first day increased and then decreased during the day. In the following days, the growth pulsations almost ceased, the colonies stopped growing, and their coenosarcs began to exfoliate from their perisarcs. However, by the fourth day, this process slowed down, and the colonies existed in an economy mode of experiencing unfavourable conditions. The thermal shock continued in the experiment for five days. Then, after the temperature dropped from 25 °C to 15–16 °C, all the colonies recovered within five days and continued to grow.

Keywords: Hydrozoa; growth pulsations; adaptation; extreme temperature; White Sea

Citation: Marfenin, N.N.; Dementyev, V.S.; Nikolaev, E.V. How Tolerant Are Hydroids to Climate-Change-Induced Acute Spikes in Sea Water Temperature? A Case Study of Arctic *Dynamena pumila* (L., 1758). *Hydrobiology* **2023**, *2*, 583–601. https://doi.org/10.3390/hydrobiology2040039

Academic Editor: Cláudia Pascoal

Received: 21 August 2023
Revised: 28 October 2023
Accepted: 6 November 2023
Published: 13 November 2023

1. Introduction

Temperature extremes are becoming increasingly common in unstable climates [1–3]. This is a public health concern [4], but for biota in general, global warming is even more dangerous and unpredictable [5–7], especially for polar ecosystems including the Arctic [1,8,9], where climate change is predicted to be stronger than at low latitudes [10].

The response to an extreme increase in environmental temperature is not known for most species [6,11]. For a number of species, a few studies identified a critical temperature at which death occurs [12], but the exposure to extreme heat was short-lived. How quickly do changes in vital activity appear with a prolonged increase in temperature? To what extent are these vital reactions reversible? Is it possible to adapt to extreme conditions of existence? These and similar questions are directly related to the response of ecosystems to possible climate warming. So far, the scientific literature has been dominated by only the most general assumptions about changes in ecosystems; these assumptions are often based on biogeographic data. However, the methods of biogeography can reliably determine only the established correspondences between habitat conditions and ecosystems. In such cases, the ecological preferences of species are judged using the typical characteristics of the biotopes in which these species live within their ranges. Obviously, this method is not enough to determine the response of a species to an ongoing change in habitat indicators [13].

Therefore, we undertook an experimental study on colonial hydroids in order to determine the immediate and prolonged response of some key vital signs to a significant increase in seawater temperature.

This article presents the results of studying the reaction of *Dynamena pumila* (L., 1758 to an increase in water temperature from 14–15 °C to 24–25 °C, as well as a subsequent decrease in temperature to a normal value of 15 °C, using the species' growth and the pulsations of the body of the colony. Few studies of this kind have been performed in hydroids, all of which were scattered and gave only a general idea of the reaction of the colonies to a slight increase in water temperature [14–24]. Only recently was a study performed on the instantaneous reaction of the colonial hydroid *D. pumila* to various temperature increases, and it was found that 25 °C was the limiting temperature at which the hydroid did not die [25].

However, this is not enough to accurately determine the upper temperature limit of the survival of individuals. Now, we have determined how constant the hydroid's negative reaction to an increasing temperature is. Does adaptation to that temperature occur over a few days following a significant and rapid increase in temperature to the upper limit?

The White Sea population of *D. pumila* lives in the upper sublittoral zone and even in the drying zone during regular low tides. Only a small part of the White Sea invertebrate fauna survives such conditions. Therefore, *D. pumila* can rightfully be classified as a eurybiont. Without an accurate idea of how much sea surface temperatures will increase with the predicted warming of the global climate, it seems advisable to at least learn about the reaction of the most resilient eurybiont species to the upcoming ordeal. The first question that must be answered is what is the thermal tolerance limit of the species? Therefore, in our study, we focused on determining the upper temperature limit of the White Sea population of *D. pumila*. The most severe exposure conditions were chosen: a rapid and significant change in temperature. Having previously established [25] the upper temperature limit for *D. pumila* under such extreme conditions in an experiment on the response of the species' growth and stolon pulsations in colonies in the first hours of a sharp change in temperature, in this study, we wanted to determine how stable the cessation of growth and changes in stolon pulsations are within five days. We were also interested in the possibility of restoring the normal life activity of *D. pumila* with a subsequent decrease in water temperature and the speed of this process.

2. Materials and Methods

The object of study: the colonial hydroid *Dynamena pumila* (L., 1758), a representative of the Sertulariidae family of the Leptothecata suborder of the Hydrozoa class, was chosen for this study (Figure 1). Many studies on growth, colony integration, feeding, etc., have been carried out on this hydroid [26,27].

This study was carried out on colonies grown from individual shoots. All colonies included, in addition to the initial shoot, a short stolon less than 10 mm long with one or two young shoots on it (Figure 2). We call such colonies juvenile, contrasting them with branched–developed colonies with many stolons and shoots.

2.1. The Morphology of the Colonies

D. pumila colonies are characterised by filamentous stolons creeping along the substrate. From them, at approximately equal distances from each other (on average, 3 mm), shoots depart with a two-row opposite arrangement of hydranths in hydrothecas (Figure 1). New shoots are formed within the top of the stolon but never between shoots. The growth zones are located proximally from the apex of the stolon or shoot at a distance of approximately 0.3 mm from the apical end of the stolon/shoot (apex) [25,26].

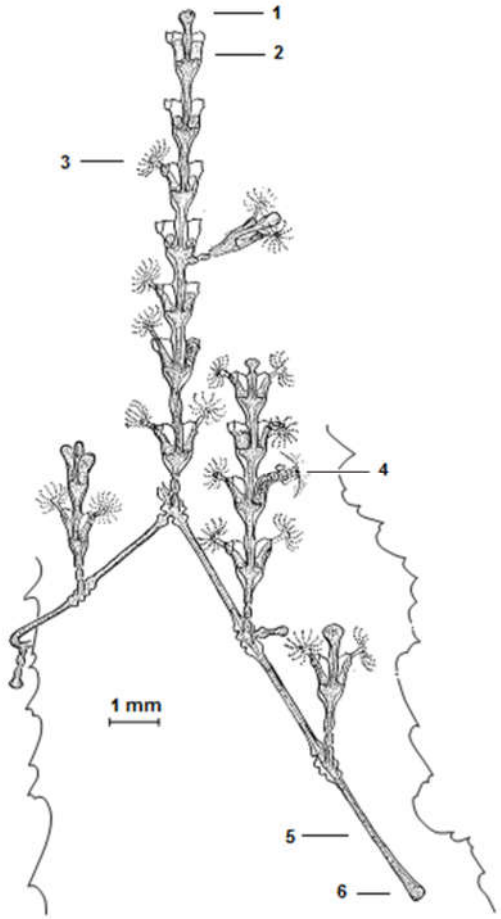

Figure 1. *Dynamena pumila* shoot morphology. Designation: 1—shoot growing tip; 2—hydrotheca; 3—corolla of hydranth tentacles; 4—hydranth swallowing nauplii; 5—stolon; 6—growing tip of the stolon.

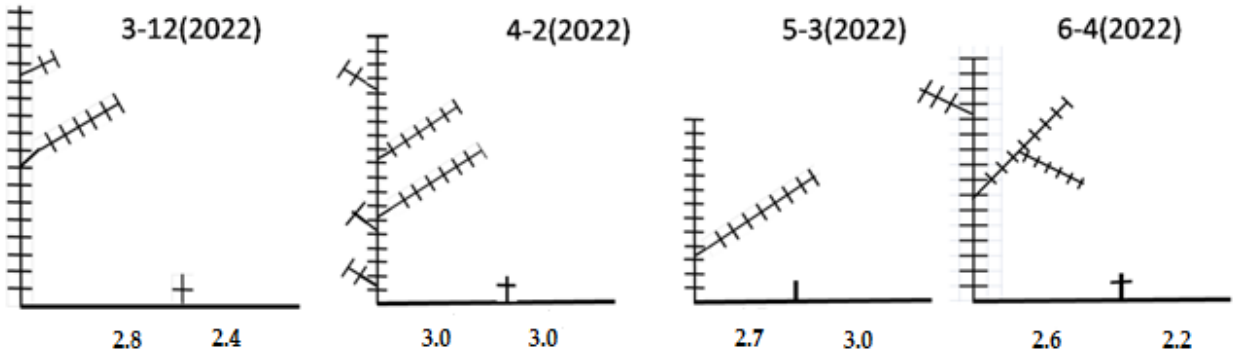

Figure 2. Schemes of young secondary (grown from individual shoots) colonies of *Dynamena pumila* used in the experiment before the increase in water temperature on 9 June 2022. The horizontal line shows the length of the stolon modules (the internodes between shoots) in mm. Pairs of hydranths on the trunks and branches of the shoots are indicated by transverse lines, and their number replaces the measurement of the shoots. Colony numbers are indicated above the diagrams.

2.2. Colony Mapping Technique

After selecting the colonies for the experiment, the registration of their sizes began: the length of the stolon, the number of shoots, the size of the shoots (expressed as the number of internodes—pairs of hydrothecas), the formation of lateral branches of the stolon, the number of active hydranths, the resorption of hydranths, and the areas of the maternal

shoot coenosarc were determined. All these indicators were obtained using a simple method of "mapping" the colonies under a binocular microscope [28], i.e., drawing up schemes of the colonies on which measurements and calculations are recorded (Figure 2).

When drawing up regular diagrams ("maps") of the colonies, we noted active hydranths, i.e., those which were not hiding in hydrothecas but had opened their tentacles. Such observations are not enough for a quantitative account; however, we used the appearance of active hydranths in colonies after they experienced unfavourable conditions as a marker for the onset of the recovery stage.

2.3. Terminology and Parameters

The text of this article uses several little-known terms and parameters which are defined below.

Colonial organism—usually called a colony, but the term colony is polysemantic; it is used to refer to both a colony of gulls or bees and to refer to modular colonial invertebrates, hydroids, corals, bryozoans, etc., although modular organisms are not communities of individuals. However, the term "colony" has become so entrenched that it is easier to use than "colonial organism". In this article, these terms are used as synonyms.

The shoot module is a part of the shoot, which in *D. pumila* includes two oppositely located hydrothecas and a section of the trunk between them. The boundaries between the modules are conditional and are "tied" to the narrowest places on the runoff between pairs of hydrothecas.

The stolon module is the part of the stolon between two successive shoots.

The growing tip is the apical (terminal) part of the coenosarc of the shoot or stolon, due to the pulsations of which this part moves forward with the stretching of the thin perisarc and the release of a new perisarc. Growing tips are morphologically different from tubular coenosarcs, which they crown.

Growth per cycle of pulsation—the distance that the top of the growth moves forward for each cycle of longitudinal pulsation.

2.4. The Collection of Colonies at Sea

D. pumila colonies live on the border of the littoral and sublittoral zones. They can be found on the macrophytes Fucus and Ascophyllum, as well as on rocks in areas of constant water movement due to regular tides [26]. In summer, the water temperature at the sea surface reaches 16 °C, and in the apexes of bays, it reaches up to 18 °C and higher, depending on the shallowness of the water and warming up. In winter, the sea is covered with ice, and the water temperature drops to a minimum of −1.3–−1.7° C on average. The salinity of the water at the surface varies between 26‰ and below. The average daily production of phytoplankton in the White Sea is 250 mg C/m^2, and the average biomass of zooplankton is about 200 mg/m^3 [29,30].

Material was collected from a dense population of *D. pumila* on the Yeremeevsky threshold (66°33.3′ N 33°08′ E) in the Great Salma Strait of the Kandalaksha Bay, near the White Sea Biological Station of Lomonosov Moscow State University, where this study was carried out [31].

During the low water phase on 2 June 2022, one bush of *Fucus serratus* on the Yeremeevsky threshold, with clean, slightly overgrown colonies of *D. pumila* was selected, and medium-sized shoots were cut from it, i.e., from 13 to 20 internodes of the shoot trunk. The shoots were fixed one by one under transverse threads on slides according to the method described earlier [32,33].

2.5. The Cultivation of Colonies

Individual shoots were placed on glass slides or on photographic plates without an emulsion (9 cm × 12 cm in size) [34,35]. The slides with *D. pumila* shoots attached to them were placed in a ten-litre aquarium placed in a large, opaque container filled with water. Water was constantly pumped (300 L/h) through a flow cooler (Resun CL–

200). So, in a container with an aquarium, a predetermined temperature of 14–15 °C was maintained, which is optimal for the rapid growth of this species [25]. With the help of a microcompressor, the water in the aquarium was constantly aerated, mainly in order to set it in motion, simulating a flow.

The colonies were fed daily with freshly hatched *Artemia salina* nauplii for one hour in a separate feed tank. The water in the aquarium was renewed daily, and the aquarium was rinsed with fresh water before it was filled with fresh sea water. *Artemia* nauplii were added to the fresh water. After feeding, the concentration of nauplii was 0.6–1.7 ind./mL.

A few days after the start of cultivation, from the bases of some cut-off shoots, which we call "mother" shoots, stolons began to grow which spread along the surface of the substrate and were firmly attached to it. After another day or two, one daughter shoot appeared on the stolons. Not all colonies were suitable for detailed study. First of all, they differed in their similarity to each other in size, depending on the date of the initiation of stolon growth. However, all grown colonies were in the experiment. From these, if necessary, it was possible to choose a replacement for a damaged colony.

2.6. The Main Stages of the Experiment

This experiment consisted of six main stages.

Stage 1: The completion of colony cultivation at 14 °C, drawing up colony diagrams, and obtaining time-lapse photographs of the pulsations of the stolon tips;

Stage 2: Increasing the water temperature to 25 °C in 2–3 h to simulate thermal shock "in its pure form", not smoothed out via a slow transition and without an adaptation to changes in temperature conditions;

Stage 3: Drawing up diagrams of the colonies and obtaining time-lapse photographs of the pulsations of the tops of the stolons immediately after increasing the water temperature to record the rapid responses of the growth and pulsations of the coenosarcs of the colonies to thermal shock;

Stage 4: Drawing up diagrams of the colonies and obtaining time-lapse photographs of the pulsations at the tops of the stolons twice over five days to detect a possible adaptation to elevated water temperatures;

Stage 5: Reducing the water temperature from 25 °C to 15–16 °C within 2–3 h, recording changes in the structure of the colonies and obtaining time-lapse photographs of the pulsations of the tops of the stolons to determine the immediate reaction of the colonies to the restoration of growth conditions typical for this species in the White Sea;

Stage 6: Recording changes in the structure of colonies and conducting time-lapse photography of pulsations at the tops of stolons on the fifth day of keeping colonies under normal cultivation conditions to determine the degree of restoration of the growth and pulsations of stolons after a five-day thermal shock.

2.7. Time-Lapse Microvideo Recording Technique

Time-lapse microvideos were filmed to register the vital signs of the *D. pumila* colonies. For this, an Arecont AV3100M video camera was fixed on a microscope tube and connected to a personal computer. Filming was carried out frame by frame with a frequency of 4 frames/s. A transparent cuvette with double walls and a bottom was placed on the working table of the microscope. The inner volume was a working space filled with fresh sea water in which to place glass with colonies to videorecording, and the outer space between the two walls and two bottoms was used to achieve a constant flow of water of a certain temperature which was pumped through the flow cooler. Taking into account the size of the cuvette, it was the most convenient to use the simplest microscope, an MBI-1 with a straight tube, on which a video camera was fixed. The object was illuminated using a separate illuminator, the beam of which was directed into the field of view through a mirror. This helped avoid overheating the working area during filming. For microscopy, an 8× microscope objective without an eyepiece was used. Due to the tube, the overall increase was approximately 100-fold. Before shooting the object, a scale microline was

taken which was used to calibrate the on-screen ruler for subsequent measurements during the cameral processing of the video recordings.

Time-lapse photography makes it possible to register (1) growth of the stolon apex, (2) the pulsations of the apex, and (3) coenosarc walls in any transparent place of the stolon, as well as (4) the movement of particles in the gastrovascular cavity of the stolon which are carried by hydroplasma (internal fluid filling the cavity).

The pulsations of the coenosarc can be express indicators of the state of a colonial organism of hydroids. The most sensitive and reliable among all indicators of coenosarc pulsation are the regular successive protrusions and contractions of the terminal end of the apex of a stolon or shoot, which are usually called growth pulsations or pulsations of the growth apex [34,35]. Normally, growth pulsations are rhythmic and can be characterised by several indicators, including their period, amplitude, and growth per pulsation cycle. Although these indicators do not remain strictly constant, they are nevertheless convenient for comparison, including graphical comparisons. The growth pulsation plots clearly show differences in detail. More information can be extracted from them than from averaging, but to achieve this, it is necessary to analyse growth pulsations individually for colonies.

The video recordings were decoded using the following method. In order to register the processes in an accelerated mode corresponding to a half-minute interval, every 30 s, three indicators were measured on a computer monitor with a screen microline: (1) the position of the apical edge of the stolon apex, (2) the size of the coenosarc lumen, and (3) the displacement of any distinct particles in the colony cavity within the field of view. The results of registering the speed of particle movement are not given in this article. Based on the measurements of the position of the apical point of the apex of the stolon coenosarc, the increase in one cycle of pulsations was determined. With the degradation of the apex and its departure from the perisarc, the growth rate turned out to be conditional because while pulsing, the stolon did not grow, and the tip only moved forward inside the empty space in the perisarc from time to time.

2.8. Statistical Processing

Since the distribution of quantitative data often differs from a normal distribution, we used the median to estimate the average values, and the quartiles Q1 and Q3 were used to determine the degree of deviation from the average values. The significance of differences between samples was determined using the Mann–Whitney U test.

The samples depended on the number of pulsations taken into account, and they, in turn, depended on the pulsation frequency and the total recording time. The standard shooting time was 90 min, but nighttime was also used, so individual episodes lasted from seven to nine hours.

2.9. The Number of Colonies in the Experiment

Our experience, gained from many years of research, suggests that the samples in the study of the growth, resorption, and functioning of the distribution system should be small in order to be able to individually analyse the processes studied in each colony, along with statistical processing [25,27,35]. Modular and especially branched organisms differ from each other incomparably more than unitary (single) organisms [27]. These differences are not limited to age and environmental factors. For example, the intensity of the branching of shoots and stolons affects the growth rate and the nature of the functioning of the distribution system. No less influence is exerted by the processes of the resorption of hydranths, depending on a set of circumstances. Therefore, during a study, one should strive not to increase the sample and limit the parameters but to ensure a comprehensive individual consideration of a variety of indicators, using the example of the optimal number of individuals. This approach is called “idiographic” [35].

Of the several dozen cut-off shoots of *D. pumila*, only a third attached to glass and produced a stolon, and not all of them began to grow stolons convenient for subsequent observations, i.e., stolons which were straightforward and without branching. Therefore,

the experimental sample included colonies in which the formation of stolons was not delayed and the direction of their growth was convenient for observation. There were no other criteria for selecting colonies for this experiment. Therefore, the colonies were not uniform, although they were similar to each other (Figure 2). Such limited heterogeneity is best suited to an individual analysis of the dynamics of indicators over the course of an experiment within a small group of related research objects.

Initially, there were five *D. pumila* colonies in the experiment, but over the course of the experiment, one colony dropped out, and the second was replaced with an identical colony in the first days of the experiment. The limitation of the number of colonies allows for replacement, if necessary, since all results are tracked and compared with each other for each colony separately and not just on average. Therefore, the idiographic approach expands the possibilities of statistically processing quantitative data, especially when tracking changes that occur in objects over the course of monitoring.

3. Results

3.1. The Dynamics of the Morphological Parameters of the Colonies during the Experiment

At a temperature of 14–15 °C and in the presence of food, *D. pumila* colonies actively grow, so in one week from 2 June 2022 to 9 June 2022, the colonies formed 5 mm long stolons attached to the substrate on which a shoot germ appeared (Table 1). In such colonies, almost all hydranths are located on mother shoots because there are still very few of them on new shoots.

Table 1. The dynamics of indicators: stolon length, the number of shoots, the number of growing shoot tips, and the number of pairs of hydranths in five colonies of *Dynamena pumila*, depending on the water temperature in the experiment. Designations: Me—median, Q1—25% quartile, Q2—75% quartile.

Date		9 June 2022	11 June 2022	14 June 2022	17 June 2022	20 June 2022	21 June 2022	22 June 2022	23 June 2022	24 June 2022
Temperature, °C		13.9	25.1	24.4	15.9	15.2	15.1	15.1	15.1	15.2
Length of the stolon, mm	**Me**	**5.0**	**6.5**	**7.2**	**8.1**	**10.4**	**11.0**	**11.7**	**12.5**	**13.1**
	Q1	4.8	6.1	6.4	7.5	9.4	10.0	10.5	11.3	11.9
	Q3	5.3	6.8	7.8	9.2	11.6	12.2	12.9	13.6	14.3
Number of growing tips on the shoot	**Me**	**1.0**	**2.0**	**2.0**	**2.0**	**3.0**	**3.0**	**3.5**	**4.0**	**4.0**
	Q1	1.0	2.0	2.0	2.0	3.0	3.0	3.0	4.0	4.0
	Q3	1.0	2.0	2.0	2.3	3.3	3.3	4.0	4.0	4.0
The number of pairs of hydranths in young shoots	**Me**	**1.0**	**2.0**	**2.5**	**4.0**	**8.5**	**8.5**	**8.5**	**9.0**	**9.5**
	Q1	0.8	1.8	2.0	3.8	7.8	7.8	7.8	8.8	9.0
	Q3	1.0	2.0	3.0	4.3	9.0	9.0	9.3	9.3	10.0

On ***9 June 2022***, at a temperature of 14 °C, the terminal pulsations of the stolon tips were recorded. These conditions are optimal for the growth of D. pumila colonies. These indicators of stolon pulsations were considered a control, and the results of all subsequent days of the experiment were compared with them.

On ***10 June 2022***, the water temperature in the aquarium with the colonies was increased from 14–15 °C to 24–25 °C, and a survey was conducted to record the immediate reaction of the colonies to such a strong increase in temperature. A day later, all colonies showed an increase in the length of their stolons and the formation of one more shoot (Table 1).

Further, from ***11 June to 15 June at 25 °C***, growth in all colonies stopped, which can be judged using the colony mapping carried out on 14 June 2022 (Table 1), as well as the state of the growing tips of the stolons. The schemes of the colonies show that they remained the same in terms of the length of the stolons and the size of the shoots as on 11 June 2022, i.e., these dimensions did not increase during the 5 days of thermal shock, but not a single colony resolved during the time of maintaining the temperature at 25 °C.

On the last day of thermal shock, i.e., on ***14 June2022***, during mapping after feeding, individual hydranths with extended tentacle corollas were visible in all colonies: there were from two to twelve hydranths per colony, some of which had anchored *Artemia* nauplii.

Therefore, a few days after the end of the thermal shock, the colonies could feed, although on previous days, for example, on ***11 June 2022***, no straightened hydranths were seen.

After ***15 June 2022***, when the temperature in the aquarium with hydroids was lowered from 25 °C to 15 °C, during the next colony mapping on ***17 June 2022***, the growth of stolons and shoots was restored in all colonies. The growth of the colonies continued further. For 10 days of maintaining the colonies at 15 °C after the completion of a five-day thermal shock, the length of the stolons and the number of shoots doubled (Table 1), and the number of hydranths in young shoots increased by four times.

3.2. The Dynamics of Indicators of the Pulsation of the Coenosarc with a Change in Temperature

The growing tip is the apical (terminal) part of the coenosarc of a shoot or stolon, due to the pulsations of which this part moves forward with the stretching of the thin perisarc and the release of a new perisarc. Growing tips are morphologically different from the tubular coenosarc they crown.

Control stage (14–15 °C), 9 June 2022: Under normal temperature conditions at 14–15 °C, the terminal pulsations of the growing tips were rhythmic, with average (x ± SD) indicator values: a period of 14.4 ± 6.5 min, an amplitude of 15.8 ± 9.5 µm, a gain per cycle of 7.0 ± 4.7 µm, and a resting phase of 81.7% (Table 2). The interquartile range (Q3—Q1) allows for a clearer representation of the degree of the spread of the values. The rhythm was not equally expressed in the four experimental colonies. Colony No. 5-3 differed from the others (Figure 3). Its growth apex pulsation amplitude was less than that of the others, although its other indicators did not differ from those of the other three colonies. The terminal pulsations of the stolon tips at 15 °C are mainly represented by the resting phase, when the apical edge remains in the same position at both maximum compression and maximum extension. The resting phase lasts for almost 82% of the time, and the apical protrusion phase is almost twice as long as the compression phase (11.0 and 7.3%, respectively).

Table 2. The dynamics of indicators: the period and amplitude of pulsations of the stolon apex and the stolon growth per hour, as well as indicators of the proportion (%) of resting phases and the extension and compression of terminal pulsations of the stolon apex in colonies as the water temperature changes. Designations: Me—median, Q1—25% quartile, Q2—75% quartile.

Date		9 June 2022	10 June 2022	11 June 2022	12 June 2022	13 June 2022	14 June 2022	20 June 2022	21 June 2022	22 June 2022	23 June 2022	24 June 2022
Temperature	°C	13.9	23.3	25.1	24.4	24.7	24.2	15.2	15.1	15.1	15.1	15.2
Period, min	**Me**	**14.0**	**7.5**	**8.0**	**8.5**	**9.0**	**8.5**	**17.0**	**16.5**	**17.0**	**16.5**	**16.0**
	Q1	12.1	7.0	7.5	6.6	8.0	7.1	16.5	15.4	16.1	14.5	14.8
	Q3	15.9	8.5	8.7	10.0	11.5	13.6	17.5	18.1	18.4	17.5	17.0
Amplitude, µm	**Me**	**15.3**	**19.5**	**16.0**	**4.2**	**9.7**	**11.1**	**24.4**	**24.4**	**30.6**	**37.6**	**39.3**
	Q1	8.9	13.2	9.7	0.0	4.9	8.4	11.8	18.8	22.6	23.5	27.8
	Q3	21.8	23.3	27.1	9.7	15.7	18.8	32.7	41.8	40.0	52.5	47.3
Stolon increase per hour, µm/h	**Me**	**16.0**	**42.8**	**28.2**	**−12.9**	**−13.8**	**−5.6**	**25.8**	**34.5**	**43.5**	**40.7**	**40.0**
	Q1	10.4	31.5	18.4	−23.3	−29.7	−7.8	24.4	31.8	32.0	36.5	28.7
	Q3	27.7	62.1	39.8	−3.0	3.8	1.2	39.3	38.6	58.3	47.5	49.4
Pulsation relaxation phase	%	81.7	74.8	75.5	87.8	87.2	87.6	81.1	81.2	80.7	83.0	81.6
Pulsation expansion phase	%	11.0	14.0	12.8	5.1	5.3	5.6	11.3	11.8	12.0	10.8	11.2
Pulsation contraction phase	%	7.3	11.2	11.7	7.1	7.5	6.8	7.6	7.0	7.3	6.2	7.2

On 10 June 2022, an increase in temperature to 25 °C represented the first day of thermal shock. With an increase in the seawater temperature of 10 °C (from 14–15 °C to 25 °C) within 1–2 h, the main indicators of pulsations—the period, amplitude, and increase—changed literally over several cycles of the expansion and contraction of the stolon tip. Comparing the graphs of growth pulsations (Figure 3) before (A) and after (B) the increase in water temperature, it can be seen that the frequency of pulsations increased significantly in all stolons. At the same time, the growth rate increased. The growth per hour increased by an average of 1.7 times ($p \leq 0.05$). The latter occurred not due to an increase in growth per cycle (Table 2) but due to an increase in the number of pulsation

cycles over the same period. The pulsations became more regular in most of the colonies, and their amplitude increased in two colonies, while in the other two colonies, it remained the same. The resting phase was slightly reduced, taking up 74.8% of the time, and the contraction phase became significantly longer.

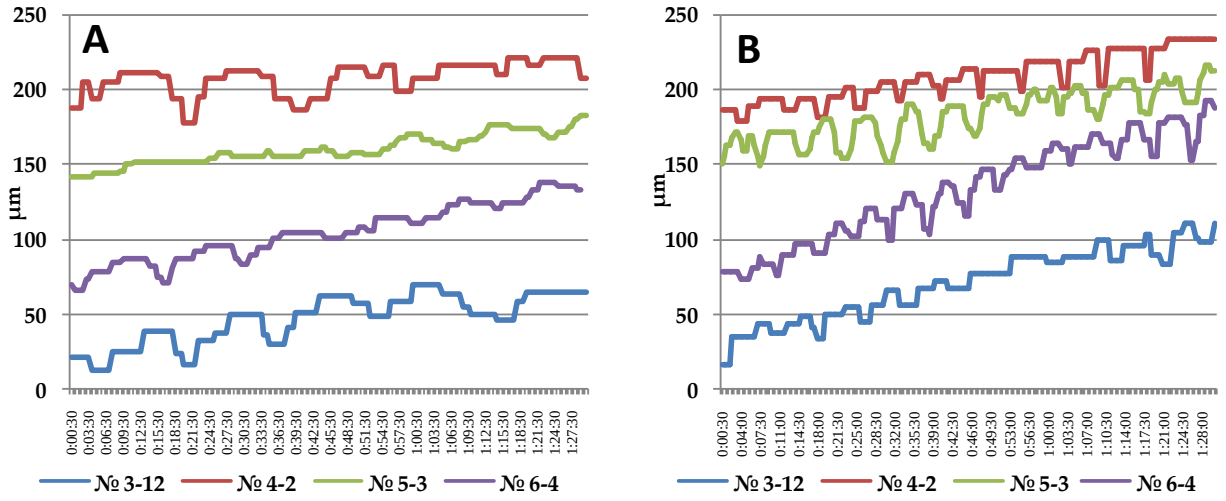

Figure 3. Terminal stolon tip pulsations in four *Dynamena pumila* colonies at 14 °C (**A**) and 2 h 47 min (**B**) after the sea water temperature rose to 23.9 °C. The first day of thermal shock. The duration of filming was 1 h 30 min each. On the "X" axis is the time from the beginning of the experiment (h:m).

The second day at 25 °C occurred on 11 June 2022 (Figure 4). Over the next 24 h, the pulsation frequency did not change, and the growth of the stolon apex per hour decreased by 1.5–1.6 times. The amplitude of the pulsations did not change, although it became unstable, which is clearly visible in both the pulsation graphs (Figure 3) and the increase in the interquartile range (Table 2). The ratio of the phases of rest, compression, and expansion remained the same after the increase in water temperature on 10 June 22, i.e., the resting phase remained shortened, mainly due to some increase in the compression phase.

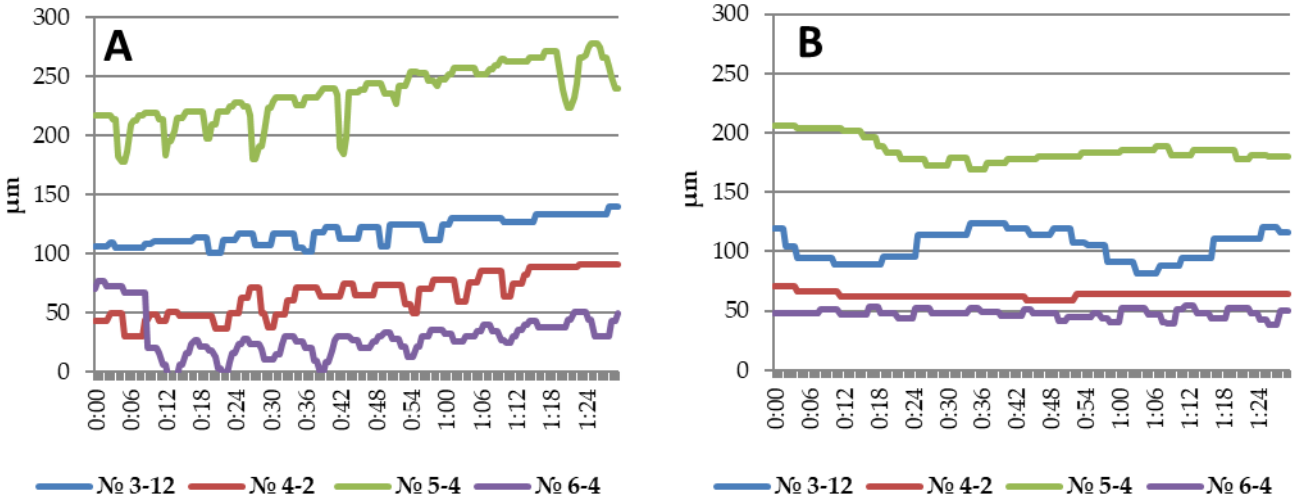

Figure 4. The terminal pulsations of stolon tips in four colonies of *Dynamena pumila* (**A**) on the second day and (**B**) on the third day of thermal shock. On the "X" axis is the time from the beginning of the experiment (h:m).

The third day at 25 °C occurred on 12 June 2022 (Figure 4). The tips of the stolons in all colonies stopped growing, but the pulsations persisted. The tips of the stolons were already loosely attached to the perisarc, and the stretched coenosarc pulled them inside the perisarcal tube (Figure 5). This most clearly indicates a halt in growth. The stages of growth were replaced by stages of compression (departure from the perisarc) of the apex of the stolon. Then, the elongation of the stolon apex resumed temporarily within the already formed perisarc, and compression set in again (Figures 4 and 5).

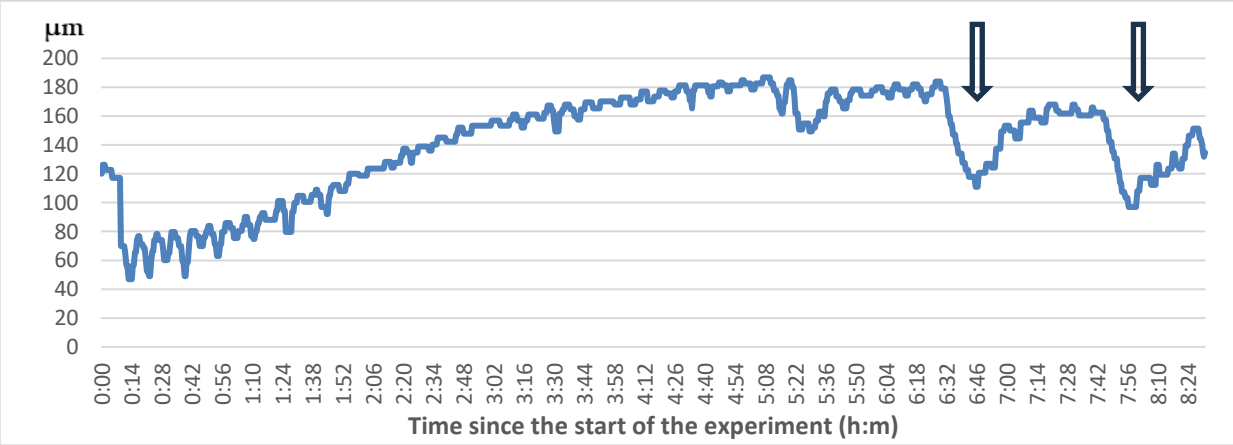

Figure 5. The pulsations of the top of the stolon of the *Dynamena pumila* colony No. 6-4. Filming time: 8 h 27 min. Arrows indicate sharp displacements of the growing tip from the end of the perisarcal tube of the stolon.

The averaged values of the period of the pulsations give only an approximate idea of the increase in the variability of the duration of the pulsations and the gradual decrease in the frequency of the pulsations (Table 2). An individual analysis of the colonies makes it possible to extract more information (Figure 4). The periodicity of the pulsations in one of the colonies was completely disturbed, while in the other, it was weakly manifested. In the other two colonies, the terminal stolon pulsations were still periodic, although they look like distorted pulsations on the graphs, with the presence of expansion but the absence of compression or vice versa—colony No. 3-12.

The amplitude of the terminal pulsations decreased by 3.8 times ($p \leq 0.01$), remaining highly variable (Table 2). Now, the stolons did not lengthen but shortened. The ratio of the phases of the pulsations on the third day of thermal shock changed dramatically. The rest phase was lengthened, while the stretching and contracting phases were shortened, but this does not indicate an acceleration of the expansion and contraction processes—the reason is a decrease in amplitude, i.e., the duration of contraction and expansion from maximum to minimum. The pulsations became less active.

On **13 June 2022, the fourth day at 25 °C** (Figure 6), the terminal pulsations of the stolon tips of the four colonies were not similar to each other.

In colony No. 3-12, the amplitude of the pulsations increased and then sharply decreased.

In colony No. 4-2, the dormant period was replaced by terminal apical pulsations and a loss of connection between the coenosarc and the perisarc, with a concomitant posterior displacement from the end section of the perisarcal sheath.

In colony No. 5-4, after moving away from the end of the perisarc, the terminal pulsations almost ceased. In the video, it is noticeable that the top of the coenosarc weakly pulsates, but this is not expressed in regular longitudinal oscillations.

In colony No. 6-4, a long dormant stage was replaced by a retreat of the apex coenosarc from the end of the perisarc and the initiation of weak pulsations.

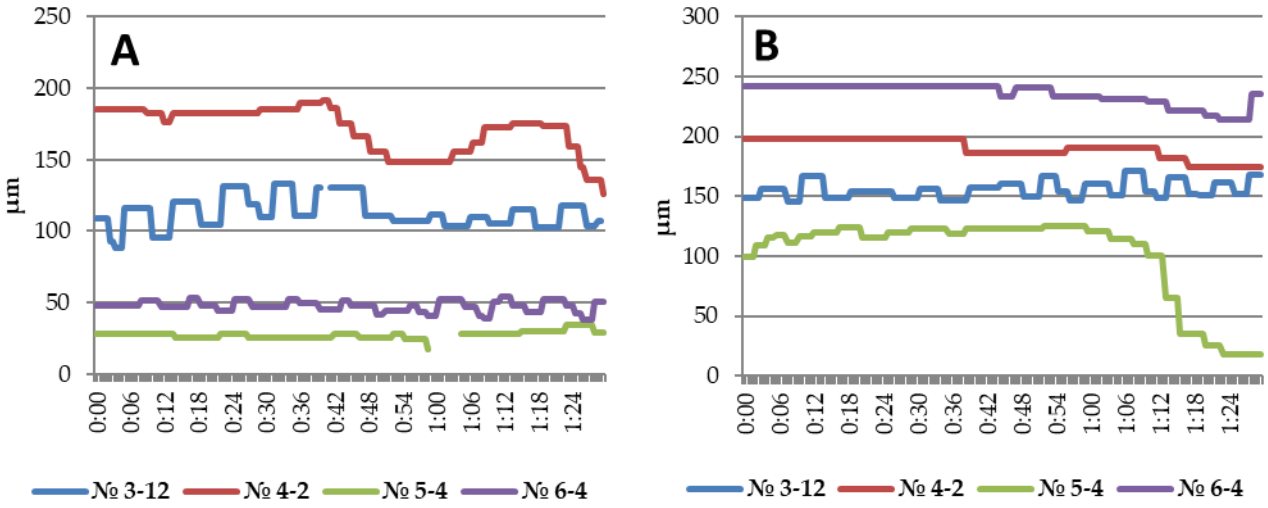

Figure 6. The terminal pulsations of stolon tips in four colonies of *D. pumila* (**A**) on the fourth day and (**B**) on the fifth day of thermal shock. On the "X" axis is the time from the beginning of the experiment (h:m).

Formally, the averaged indicators reflect the general pattern (Table 2). The period of the pulsations remained the same as the previous day. The pulsation amplitude increased. The stolon growth rate per hour became negative. The resting phase remained maximal, while the expansion and contraction phases were minimal, with expansion taking less time than contraction, which is different from normal at 14 °C.

In fact, the main result on the fourth day of thermal shock was the imbalance in the terminal pulsations, which can be clearly seen on individual graphs and when comparing the pulsation graphs for the four colonies.

On the fifth day at 25 °C (Figure 6), 14 June 2022, terminal pulsations were restored in two colonies out of four, moreover, the pulsations were restored with different periods. Their tops began to move forward inside the perisarcal tube. This was not growth yet but a restoration, at least partial, of the previous positions. The degradation process continued in the other two colonies: the tops receded and the pulsations became irregular, with varying periods and amplitudes.

The instability of the terminal pulsations of the stolon apex on the fifth day of thermal shock can be seen especially clearly in the footage from a prolonged, 9.5 h recording in colony No. 4-2. During this time, the direction of the movement of the stolon tip, the period, and the amplitude changed (Figure 7).

Recovery after thermal shock

After a rapid decrease in sea water temperature to 15 °C on the fifth day after the start of the experiment, the process of colony recovery began. During the first five days of colony recovery, the registration of growth pulsations was not carried out and was resumed on the sixth day (20 June 2022) of colony maintenance at 15–16 °C. By this time, stolon growth had resumed in all colonies (Table 1), and the growth pulsations became more rhythmic (Figure 8). Daily time-lapse microvideo filming, starting from the eleventh day of the experiment (the sixth day of recovery at 15 °C), made it possible to track the rehabilitation process.

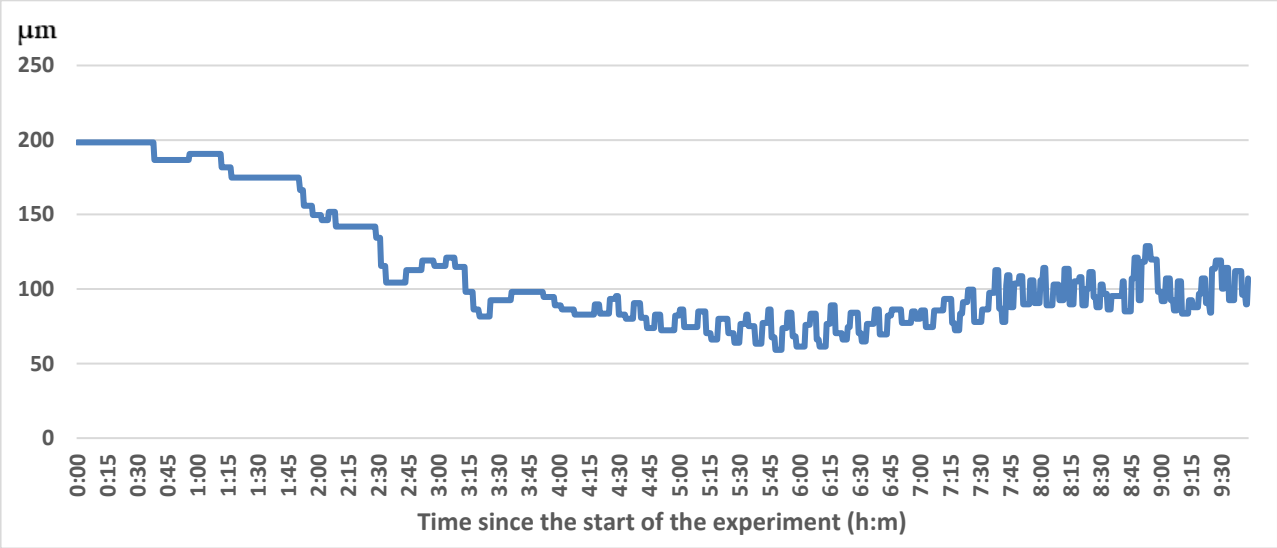

Figure 7. Pulsations of the apex of the stolon of *Dynamena pumila* No. 4-2 on the fifth day after the increase in water temperature. T = 24.4 °C. Filming duration: 9.5 h.

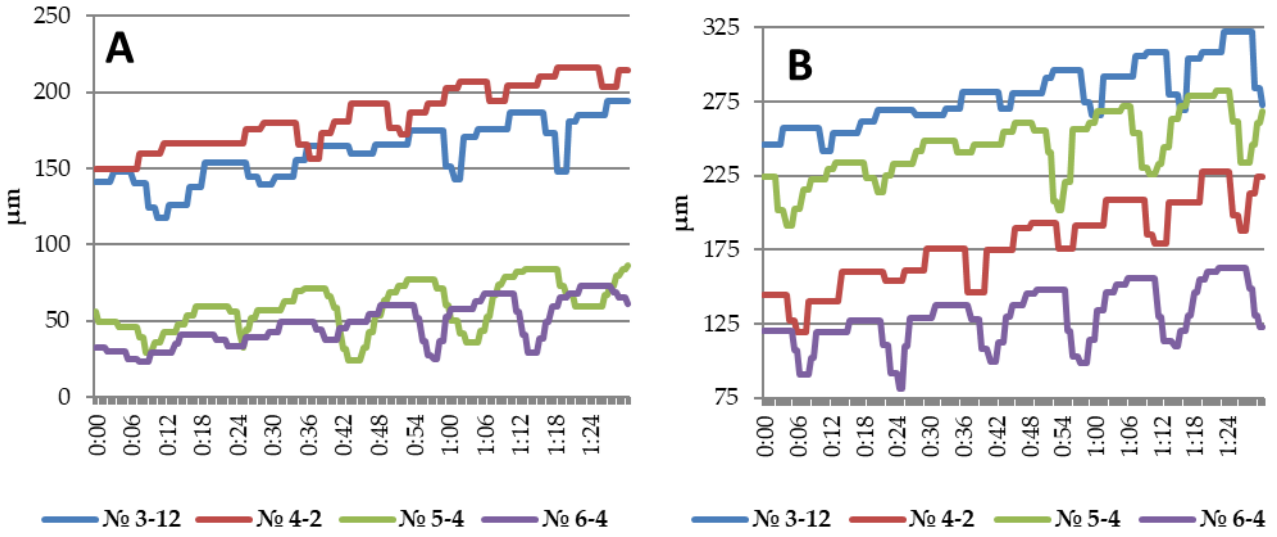

Figure 8. The terminal stolon tip pulsations in four *Dynamena pumila* colonies (**A**) on the sixth day and (**B**) on the tenth day of recovery at 15–16 °C. On the "X" axis is the time from the beginning of the experiment (h:m).

On **20 June 2022,** the **sixth day at 15–16 °C**, in all four colonies, the pulsations of the stolon tips were restored (Figure 8). The pulsation period became longer than at the beginning of the experiment at 14 °C (Table 2). The amplitude of the pulsations increased but due to significant variations, the difference from the amplitude at the end of the thermal shock stage turned out to be less clearly expressed ($p \leq 0.05$). The growth of the colonies not only recovered but also intensified. The increase in the stolon per hour exceeded the initial values at the beginning of the experiment at 14 °C ($p \leq 0.05$). The ratio of the phases of rest and the stretching of the stolon tip and its compression became the same as at the beginning of the experiment. The extension phase was almost twice as long as the compression phase, which is typical of normal growth pulsations.

On **24 June 2022, the tenth day at 15–16 °C** (Figure 8), the pulsations almost did not differ from the previous ones on 20 June 2022. All the experimental colonies had normal terminal pulsations. Variations in pulsations when comparing colonies were insignificant.

The period remained unchanged, slightly exceeding the period at the beginning of the experiment ($p \leq 0.05$) (Table 2). The amplitude increased every day from 20 July to 24 July, eventually exceeding the value at the beginning of the experiment by 2.5 times ($p < 0.01$). The increments per pulsation cycle and per hour did not change compared to 20 June 2022 and remained higher ($p \leq 0.05$) than at the beginning of the experiment (Table 2). The ratio of the phases of rest and the extension of the stolon apex and its compression remained unchanged during the five days of recording pulsations during the recovery period of the colonies (from 20 June 2022 to 24 June 2022).

An individual analysis of the pulsations of the four colonies at the recovery stage did not reveal significant differences between them. The uniformity of terminal pulsations is a sign of colony recovery after a thermal shock.

The results of the entire experiment, from 9 July to 24 July 2022:

- A reduction and, most importantly, imbalance in the pulsation period when the water temperature increased from 14 °C to 25 °C;
- A decrease in the amplitude of the pulsations with a two-day delay relative to the onset of thermal shock;
- An increase in the amplitude of the pulsations at the stage of colony recovery at 15–16 °C;
- The complete recovery of the pulsation period by the sixth day of maintaining the temperature at 15–16 °C;
- Stable growth per hour with the recovery of the colony after five days at a temperature of 15–16 °C;
- The restoration of the normal ratio of the durations of the pulsation phases of the tips of the stolons by the fifth day of keeping the colonies at 15–16 °C. The restoration of the normal ratio of the durations of the pulsation phases of the stolon tips by the fifth day of keeping colonies at 15–16 °C.

4. Discussion

In connection with global climate change and increases in the temperature of the upper water layer recorded in a number of locations [36,37], the timely determination of changes in species' ranges is especially important [38]. Understanding and scientific forecasts of the biological consequences of climate warming should be based on fundamental information about the responses of biological species to changes in environmental temperature. However, thermotolerance, the range of allowable temperature values in which the viability and temperature optimum of a species is maintained, is far from known for all species. In addition, indicators of ecological tolerance and the temperature optimum should be tested for different life cycle stages, as well as in combination with other environmental factors; this significantly increases the amount of information needed and reduces the number of species for which all or at least a significant part of this information is already available. Such species include representatives of the class Hydrozoa: freshwater hydras [39–42] and marine colonial hydroids [14,15,17,18,31].

Among colonial hydroids, the reaction to water temperature is best studied in three species: *Cordylophora caspia* (Pallas, 1771), *Clava multicornis* (Forsskål, 1775), and *Dynamena pumila* (L., 1758).

The response of marine cnidarians to temperature depends on the salinity of the water. Therefore, most studies compare combinations of given temperature and salinity series [18,43,44]. For example, in a study of *Clava multicornis*, a hydroid's response was compared to 12 different combinations of constant temperature and salinity levels: temperatures of 12, 17, and 22 °C and salinity levels of 16, 24, 32, and 40‰.

At 12 °C and 17 °C, the colonies survived in water at any of the four salinities, and at 22 °C, most colonies survived no more than one week at 16 °C and 40 ‰ salinity.

Optimal conditions were determined using the following indicators: (a) the length and width of the body of the hydranth, (b) the number and length of tentacles, and (c) the rate of digestion. In water with a salinity of 16‰, the length of the hydranth in *C. multicornis*

reached its maximum at 12 °C, at a higher level of salinity (24‰) at 17 °C, and at a salinity of 32‰ at 22 °C. The number of tentacles on the hydranth decreased with increasing temperature and depending on salinity. The maximum number of tentacles was observed at 12 °C and 16‰, at 17 °C and 24‰, and at 22 °C and 32‰ [17]. As a result, the optimal conditions for different criteria could differ somewhat. Thus, the growth of stolons was the fastest at 12 °C and 32‰, and the highest rate of increase in the number of hydranths occurred at temperatures of 17 °C and 22 °C and a salinity of 32‰.

Cordylophora caspia grows in a wide range of aquatic environments varying in salinity, temperature, currents, oxygen, etc. Survival resistance among populations varies greatly as a result of both genetics and acclimatisation [45].

The optimal temperatures for the asexual growth of *Cordylophora caspia* were found to be 11–18 °C for populations in Germany [14,15], 18–26 °C for populations from Massachusetts, USA [46], 16–25 °C for populations in San Francisco [47], and 23–30 °C for colonies from Iraq [45]. The upper temperature limit was established in experiments to determine a means of eliminating this species in the biofouling of TPP pipelines. *C. caspia* colonies were harvested from the Des Plaines River in Joliot, Illinois, cultured under laboratory conditions in the same water, and then exposed to elevated temperatures of 35 °C for 2, 4, 6, and 8 h; 36.1 °C for 1, 3, 5, and 7 h; and 37.7 °C and 40.5 °C for 1 and 2 h. It is important that the temperature was raised at a rate of 2 °C over 15 min, i.e., not all at once, but rather quickly. At the end of the thermal shock, the colonies were transferred into an aquarium with room-temperature water (19.4 °C), and further growth or recovery was monitored by changing the number of hydranths after 7 and 12 days. In all variants of thermal shock, the colonies stopped growing, and some of the hydranths were absorbed. Only when exposed to 35 °C for several hours did regeneration occur in room-temperature water, which was noted after 7 and 12 days, but after 8 h of thermal shock at 35 °C, the colonies could not recover. After exposure to 36.1 °C, the colonies regenerated only in a series with a thermal shock duration of 1 h. In longer series, no regeneration of the colonies was observed. From the data presented, it appears that for a population of *C. caspia* from the Des Plaines River in Illinois, the upper temperature limit for short-term exposure does not exceed 35 °C [48].

When studying the thermotolerance of the colonial hydroid *Dynamena pumila* (L., 1758), the temperature limits of survival were the focus of attention [25,49,50]. The lower temperature limit can be determined biogeographically from the temperature in winter in the habitats of the *D. pumila* population. Thise research was carried out in the White Sea.

The lower water surface temperature during winter drops to (−)1.3 °C-. . .(−)1.7 °C. However, when the water drained during low tides, *D. pumila* colonies living on fucus and stones in the zone of the boundary of the lower littoral and sublittoral can also be exposed to lower air temperatures. Usually, the inhabitants of the lower littoral are protected from freezing by thick ice covering the White Sea, but in bare areas of the littoral on rapids (for example, on the Yeremeevsky threshold in the Great Salma of the Kandalaksha Bay), the colonies remain drained at air temperatures down to −20 °C [51].

When keeping *D. pumila* colonies in the laboratory at temperatures from (−)1 °C to +1 °C, and from +1 °C to +4 °C, it was found that only a part of the hydranths remained active in winter colonies. Their size was about two times smaller than that of summer colonies, and the diameter of the corolla of the tentacles was three times smaller. With an increase in water temperature, the growth of stolons began, regardless of the amount of food received. At the same time, shoot growth under these conditions began only in the presence of food [52]. With daily feeding in water at different temperatures in four parallel series, 20 °C (13 colonies), 12 °C (10 colonies), 6 °C (18 colonies), and from −1 °C to +1 °C (5 colonies), the average growth rate of the shoots and stolons was determined via regular colony mapping. The appearance of gonophores was also recorded. The dependence of the average growth rate of shoots and stolons on the temperature in the range of 6–20 °C was close to directly proportional, while the growth rate of stolons differed when comparing colonies from different temperature conditions and was twice as fast as the growth rate of

shoots. At temperatures below 2 °C, there were few growing tops in the colonies, both in the lab and in the sea. The temperature in the area drained at low tide did not remain constant. At temperatures close to 0 °C, growing stolons elongated very slowly (0.04 mm/day), and shoots behaved similarly (0.04–0.05 mm/day) [19].

The upper temperature limit for the normal life activity of *D. pumila* was established using time-lapse microvideo recording by analysing the growth pulsations of the stolon coenosarc [25]. This method is so sensitive that it allows for the registration of changes in the growth of the coenosarc in less than two hours after the onset of exposure to environmental factors; in this case, after an increase in water temperature. It turned out that the optimal range, in which a high growth rate, intense movement of hydroplasma, and the largest volume of transferred hydroplasma are observed, is limited by the interval from 10 °C to 20 °C. At 28 °C, the pulsations of the stolon coenosarc became unstable, growth, as a rule, slowed down, and the movements of the hydroplasma were less active [25]. Therefore, the upper temperature limit of the normal life activity of White Sea *D. pumila* colonies, according to the results of the analysis of coenosarc pulsations, can be within 25–28 °C. In the natural habitat of *D. pumila* in the White Sea, the temperature of the surface meter layer of the water does not exceed 18 °C. It is under these conditions that the population of this species lives, and these conditions were used for cultivating colonies in the laboratory at 14–16 °C.

Our new experiment aimed to elucidate the possibility of the *D. pumila* colonies adapting to a rapid increase in environmental temperature within five days. If, in the previous study [25], the majority of attention was paid to the possibility of quickly registering the reaction of the colony to temperature changes, we are now interested, first of all, in the degree of sufficiency of express diagnostics for determining the long-term response of the body to the temperature increase produced in the experiment.

In all colonies that were tested using a significant increase in water temperature (an increase of 10–11 °C), growth pulsations and growth as a whole in the first hours of thermal shock were preserved, although the pulsation indexes immediately changed (Figure 3). Starting from the second or third day, the increase decreased and stopped, and the terminal pulsations of the stolon tips ceased to be regular (Figure 5). The amplitude of the growth pulsations was not strictly constant in the norm, and now it changed significantly. Also, the gain per pulsation cycle varied from normal to zero or even became negative.

Already at this phase, in some colonies, the growth of the stolon stopped. The coenosarc of the growing tip of the stolon lost its strong connection with the perisarc, and since there was often tension in the coenosarc behind the growing tip, the tip was pulled back as soon as it became thinner and shorter. Then, a gap was formed between the apex of the perisarc and the coenosarc of the stolon which was minimal in some colonies and significant in others. The change in the position of the stolon apex was now determined via two factors: the force of forward movement during the pulsations of the growth apex and the tension force of the coenosarc of the stolon which, apparently, was determined by a lack of cells in the epithelium of the walls of the body [53].

We set the duration of the thermal shock to only 5 days, during which no adaptation to a temperature of 25 °C occurred. This means that the changes in the growth indicators and the pulsations of the stolon apex obtained immediately after the increase in water temperature via the express method of time-lapse recording the stolon growth pulsations [25] can be extrapolated to at least the next 5 days (Figure 3, Table 2). Therefore, this method is quite suitable for the rapid monitoring of the effect of water warming on the state of bioassay objects such as the colonial hydroid *D. pumila*.

However, it should be taken into account that all colonies survived at 25 °C for five days, and with the subsequent cooling of the water in which they were kept, they were able to quickly recover. We did not expect recovery to begin immediately after the water temperature dropped and kept the colonies at 15–16 °C for the next five days before resuming the time-lapse recording of coenosarc pulsations. By this time, the tops of the stolons had all returned to their normal state, the coenosarc moved close to the

previously formed perisarc, and the growth of stolons resumed (Table 2). Therefore, even with prolonged exposure to elevated temperatures (up to 25 °C), the *D. pumila* population retained the ability to quickly recover when the temperature dropped.

Is this enough for the White Sea population of *D. pumila* to withstand climate warming? Currently, the maximum annual summer water temperature in the surface layer in the habitat of the White Sea population of *D. pumila* reaches 17–18 °C in July–August in some years, according to long-term measurement data.

Unfortunately, for the vast majority of species, the maximum water temperatures in their habitats are still not known. It is possible to approximately determine the living conditions of species using only the geography of their distribution.

D. pumila is an Atlantic high boreal species [54]. The range of *D. pumila* includes the entire Atlantic coast of Europe north of the Bay of Biscay, the White and Barents Seas, the coast of the British Isles, Iceland and southern Greenland, and the Atlantic coast of Canada, i.e., waters with cold currents and summer surface temperatures that are about the same (less than 19 °C) as in the White Sea [55,56].

Previously, we experimentally established that when *D. pumila* was cultivated at 15 °C in White Sea water and the water temperature was increased rapidly for several hours, the maximum level of thermotolerance in this species did not exceed 25 °C [25]. We judged this using the change in the indicators of stolon coenosarc and shoot pulsation.

This time, when investigating the reaction of *D. pumila* colonies to prolonged exposure to elevated temperature for five days, we found that immediately after the temperature was raised from 14 °C to 25 °C, the growth of colonies even increased, but not for long. The frequency of the growth pulsations of the stolon immediately increased, while the amplitude of the pulsations and the growth per cycle remained the same, which caused an acceleration in growth. A day later, and possibly earlier—during the following hours—the period of the pulsations remained reduced, and the amplitude of the pulsations decreased. The main factor is that the stolons almost stopped growing within a day after the water temperature rose to 25 °C. The pulsations became less regular, and the stolon apex coenosarc began to lose contact with the perisarc, due to which the apex "moved back". Normally, the top of the coenosarc tightly adjoins the perisarc and, pulsing, moves forward, pulling the coenosarc behind it. When growth stops and the contact surface of the coenosarc of the apex with the perisarc decreases, the coenosarc stretched behind the apex pulls it back (Figure 5). During eight and a half hours of video recording, the apex either moved forward inside the perisarcal tube or sharply moved back. Apparently, the tension of the coenosarc behind the apex became greater in these short time intervals. On the third or fourth day, the apex pulsations weakened and ceased to be regular (Figure 7). On the fifth day, the terminal pulsations became even less clear. Consequently, after five days of exposure to an elevated temperature (25 °C), adaptation did not occur in the *D. pumila* colonies.

We determined that the restoration of the pulsations and growth of colonies is possible even after five days of exposure to thermal shock. Recovery after the termination of the thermal shock occurred in just a few days. The nature of the pulsations became full-fledged in terms of their period and amplitude, and the growth rate of the stolons corresponded to the norm.

Answering the question formulated in the title of this article, it can be stated that in the stage of vegetative growth, the colonial hydroid *D. pumila* can adapt to the predicted increase in environmental temperature in the Arctic region, provided that a sufficient amount of small zooplankton, which the hydroids feed on, remains in the ecosystem. However, this conclusion is not final because the survival of the species and its ability to adapt to changing environmental conditions are not limited to the growth stage. So far, there are no data on the possibility of sexual reproduction with an increase in water temperature.

Author Contributions: Conceptualisation, methodology, supervision, writing the manuscript, editing, and funding acquisition, N.N.M.; investigation, E.V.N. and V.S.D.; video digitisation, V.S.D.; project administration, E.V.N. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Russian Science Foundation, grant number 22-24-00209, agreement dated 20 December 20 2021.

Institutional Review Board Statement: Ethical review and approval were waived for this study since the Directive 2010/63/Eu of the European Parliament and of The Council of 22 September 2010 as the protection of animals used for scientific purposes does not apply to lower invertebrates.

Informed Consent Statement: Not applicable.

Data Availability Statement: Primary data are only available upon request as authors continue to use them to prepare publications.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Easterling, D.R.; Meehl, G.A.; Parmesan, C.; Changnon, S.A.; Karl, T.R.; Mearns, L.O. Climate extremes: Observations, modeling, and impacts. *Science* **2000**, *289*, 2068–2074. [CrossRef] [PubMed]
2. Pradhan, P.; Seydewitz, T.; Zhou, B.; Lüdeke, M.K.B.; Kropp, J.P. Climate extremes are becoming more frequent, Co-occurring, and persistent in Europe. *Anthr. Sci.* **2022**, *1*, 264–277. [CrossRef]
3. Ripple, W.J.; Wolf, C.; Gregg, J.W.; Levin, K.; Rockström, J.; Newsome, T.M.; Betts, M.G.; Huq, S.; Law, B.E.; Kemp, L.; et al. World scientists' warning of a climate emergency 2022. *BioScience* **2022**, *72*, 1149–1155. [CrossRef]
4. Luber, G.; McGeehin, M. Climate change and extreme heat events. *Am. J. Prev. Med.* **2008**, *35*, 429–435. [CrossRef] [PubMed]
5. Intergovernmental Panel on Climate Change (IPCC). *Climate Change 2022—Impacts, Adaptation and Vulnerability: Working Group II Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*; Cambridge University Press: Cambridge, UK, 2023; 3056p. [CrossRef]
6. Morón Lugo, S.C.; Baumeister, M.; Nour, O.M.; Wolf, F.; Stumpp, M.; Pansch, C. Warming and temperature variability determine the performance of two invertebrate predators. *Sci. Rep.* **2020**, *10*, 6780. [CrossRef] [PubMed]
7. Schrum, C.; Lowe, J.; Meier, H.E.M.; Grabemann, I.; Holt, J.; Mathis, M.; Pohlmann, T.; Skogen, M.D.; Sterl, A.; Wakelin, S. Projected Change—North Sea. In *North Sea Region Climate Change Assessment. Regional Climate Studies*; Quante, M., Colijn, F., Eds.; Springer: Cham, Switzerland, 2016; pp. 175–218. [CrossRef]
8. Falardeau, M.; Bennett, E.M. Towards integrated knowledge of climate change in Arctic marine systems: A systematic literature review of multidisciplinary research. *Arct. Sci.* **2019**, *6*, 1–23. [CrossRef]
9. Meredith, M.; Cassotta, S. Polar regions. In *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate IPCC*; Pörtner, H.O., Roberts, D.C., Masson-Delmotte, V., Zhai, P., Tignor, M., Poloczanska, E., Mintenbeck, K., Alegría, A., Nicolai, M., Okem, A., et al., Eds.; Intergovernmental Panel on Climate Change (IPCC): Geneva, Switzerland, 2019; pp. 203–320.
10. Ottersen, G.; Constable, A.J.; Hollowed, A.B.; Holsman, K.K.; Melbourne-Thomas, J.; Muelbert, M.M.C.; Skern-Mauritzen, M. Climate change impacts on polar marine ecosystems: Toward robust approaches for managing risks and uncertainties. *Front. Clim.* **2022**, *3*, 733755. [CrossRef]
11. Poloczanska, E.S.; Burrows, M.T.; Brown, C.J.; García Molinos, J.C.; Halpern, B.S.; Ehoegh-Guldberg, O.; Kappel, C.V.; Moore, P.J.; Richardson, A.J.; Schoeman, D.S.; et al. Responses of marine organisms to climate change across oceans. *Front. Mar. Sci.* **2016**, *3*, 62. [CrossRef]
12. Evans, R.G. The lethal temperatures of some common British littoral mollusks. *J. Anim. Ecol.* **1948**, *17*, 165–173. [CrossRef]
13. MacLean, S.A.; Beissinger, S.R. Species' traits as predictors of range shifts under contemporary climate change: A review and meta-analysis. *Glob. Chang. Biol.* **2017**, *23*, 4094–4105. [CrossRef]
14. Kinne, O. The effects of temperature and salinity on marine and brackish water animals. II. Salinity and temperature-salinity combinations. *Oceanogr. Mar. Biol. Annu. Rev.* **1964**, *2*, 281–339.
15. Kinne, O. Temperature: Invertebrates. In *Marine Ecology*; Kinne, O., Ed.; Vol. I. Environmental factors, Part I; Wiley: London, UK, 1970; pp. 407–514.
16. Kinne, O. Salinity: Invertebrates. In *Marine Ecology*; Kinne, O., Ed.; Vol. I. Environmental factors, Part I; Wiley: London, UK, 1971; pp. 821–995.
17. Kinne, O.; Paffenhöfer, G.-A. Hydranth Structure and Digestion Rate as a Function of Temperature and Salinity in *Clava multicornis* (Cnidaria, Hydrozoa). *Helgol. Wiss Meeresunters* **1965**, *12*, 329–341. [CrossRef]
18. Kinne, O.; Paffenhöfer, G.-A. Growth and Reproduction as a Function of Temperature and Salinity in Clava multicornis (Cnidaria, Hydrozoa). *Helgol. Wiss Meeresunters* **1966**, *13*, 62–72. [CrossRef]

19. Burykin, Y.B. Regulatory role of some environmental factors in the growth and integration of colonial hydroids. In *Theoretical and Practical Significance of Coelenterates*; Naumov, D.V., Stepanjants, S.D., Eds.; Zoological Institute of the Academy of Sciences of the USSR: Leningrad, Russia, 1980; pp. 16–19. (In Russian)
20. Labas, Y.A.; Belousov, L.V.; Badenko, L.A.; Letunov, V.N. On pulsating growth in multicellular organisms. *Reports of the Academia of Science USSR.* **1981**, *257*, 1247–1250. (In Russian)
21. Boero, F. The ecology of marine hydroids and effects of environmental factors: A review. *Mar. Ecol.* **1984**, *5*, 93–118. [CrossRef]
22. Boero, F.; Fresi, E. Zonation and evolution of a rocky bottom hydroid community. *Mar. Ecol.* **1986**, *7*, 123–150. [CrossRef]
23. Karlsen, A.G.; Marfenin, N.N. Improving the efficiency of the use of hydroids in biotesting: The choice of species, season, temperature regime. *Proc. Acad. Sci. USSR* **1988**, *2*, 198–206. (In Russian)
24. Bavestrello, G.; Puce, S.; Cerrano, C.; Zocchi, E.; Boero, N. The problem of seasonality of benthic hydroids in temperate waters. *Chem. Ecol.* **2006**, *22* (Suppl. S1), S197–S205. [CrossRef]
25. Dementyev, V.S.; Marfenin, N.N. Influence of temperature on the growth, coenosarc pulsations, and hydroplasm movement in the colonial hydroid *Dynamena pumila* (L., 1758). *Biol. Bull. Rev.* **2019**, *9*, 432–452. [CrossRef]
26. Marfenin, N.N. *Functional Morphology of Colonial Hydroids*; Zool. Institute of the Russian Academy of Sciences: St. Petersburg, Russia, 1993; pp. 1–151. (In Russian)
27. Marfenin, N.N. Decentralized organism exemplified with colonial hydroid species. *Biosphere* **2016**, *8*, 315–337. [CrossRef]
28. Marfenin, N.N. The method of mapping the spatial organization of colonial Hydrozoa and its significance in the study of parts of the colony. In *Theoretical and Practical Significance of the Coelenterates*; Naumov, D.V., Stepanjants, S.D., Eds.; Zoological Institute of the Academy of Sciences of the USSR: Leningrad, Russia, 1980; pp. 66–69. (In Russian)
29. Berger, V.Y.; Sukhotin, A.A. Biological resources of the White Sea, their production potential and rational use. *Bull. Russ. Acad. Sci.* **2010**, *80*, 968–976. (In Russian) [CrossRef]
30. Chernov, I.; Tolstikov, A. The White Sea: Available data and numerical models. *Geosciences* **2020**, *10*, 463. [CrossRef]
31. Tsetlin, A.; Zhadan, J.; Marfenin, N. (Eds.) *Flora and Fauna of the White Sea: Illustrated Atlas*; Tovarishhestvo Nauchnyh Izdanij KMK: Moscow, Russia, 2010; 470p. (In Russian)
32. Crowell, S. Differential responses of growth zones to nutritive level, age, and temperature in the colonial hydroid *Campanularia*. *J. Exp. Zool.* **1957**, *134*, 63–90. [CrossRef] [PubMed]
33. Fulton, C. Culture of a colonial hydroid under controlled conditions. *Science* **1960**, *132*, 473–474. [CrossRef]
34. Marfenin, N.N.; Dementyev, V.S. Paradox of extended flows in *Dynamena pumila* (Linnaeus, 1758) colonial hydroid. *Biol. Bull. Rev.* **2018**, *8*, 212–226. [CrossRef]
35. Marfenin, N.N.; Dementyev, V.S. Influence of food consumption on the functioning of the pulsator-reversible transport system in hydroids—An Idiographic approach. *Biol. Bull. Rev.* **2022**, *12*, 483–503. [CrossRef]
36. Tinker, J.P.; Howes, E.L. The impacts of climate change on temperature (air and sea), relevant to the coastal and marine environment around the UK. *MCCIP Sci. Rev.* **2020**, 1–32. [CrossRef]
37. Cornes, R.C.; Tinker, J.; Hermanson, L.; Oltmanns, M.; Hunter, W.R.; Lloyd-Hartley, H.; Kent, E.C.; Rabe, B.; Renshaw, R. Climate change impacts on temperature around the UK and Ireland. *MCCIP Sci. Rev.* **2023**, 18.
38. Brooker, R.W.; Travis, J.M.; Clark, E.J.; Dytham, C. Modelling species' range shifts in a changing climate: The impacts of biotic interactions, dispersal distance and the rate of climate change. *J. Theor. Biol.* **2007**, *245*, 59–65. [CrossRef]
39. Kanaev, I.I. *Hydra: Essays on the Biology of Freshwater Polyps*; Publishing House of the Academy of Sciences; USSR: Moscow, Russia, 1952; 372p. (In Russian)
40. Loomis, W.F. Environmental factors controlling growth in hydras. *J. Exp. Zool.* **1954**, *126*, 223–234. [CrossRef]
41. Schroeder, L.A.; Callaghan, W.M. Thermal tolerance and acclimation of two species of Hydra. *Limnol. Oceanogr.* **1981**, *26*, 690–696. [CrossRef]
42. Trembley, A. *Memoirs to the History of One Genus of Freshwater Polyps with Horn-Shaped Hands*; Gaisinovich, A.E., Ed.; GI Biological and Medical Literature: Moscow, Russia, 1937; pp. 1–343. (In Russian)
43. Nipper-Buscariolli, M.; Moreira, G.S. Combined effects of temperature and salinity on *Stylactis hooperi* Sigerfoos 1899 (Hydrozoa, Hydractiniidae). I. Colony growth, development of medusa buds and hydranth degeneration. *Stud. Neotrop. Fauna Environ.* **1983**, *18*, 111–120. [CrossRef]
44. Schäfer, S.; Gueroun, S.K.M.; Andrade, C.; Canning-Clode, J. Combined effects of temperature and salinity on polyps and ephyrae of *Aurelia solida* (Cnidaria: Scyphozoa). *Diversity* **2021**, *13*, 573. [CrossRef]
45. Arndt, E.A. Ecological niche of *Cordylophora caspia* (Pallas, 1771). *Limnologica* **1984**, *15*, 469–477.
46. Fulton, C. Environmental factors influencing the growth of *Cordylophora*. *J. Exp. Zool.* **1962**, *151*, 61–78. [CrossRef]
47. Meek, M.H.; Wintzer, A.P.; Wetzel, W.C.; May, B. Climate change likely to facilitate the invasion of the non-native hydroid, *Cordylophora caspia*, in the San Francisco estuary. *PLoS ONE* **2012**, *7*, e46373. [CrossRef] [PubMed]
48. Folino-Rorem, N.C.; Indelicato, J. Controlling biofouling caused by the colonial hydroid *Cordylophora caspia*. *Water Res.* **2005**, *39*, 2731–2737. [CrossRef] [PubMed]
49. Marfenin, N.N.; Dementyev, V.S. Longitudinal stolon pulsations in the colonial hydroid Dynamena pumila (Linnaeus, 1758). *Biol. Bull. Rev.* **2019**, *9*, 42–51. [CrossRef]
50. Marfenin, N.N.; Dementyev, V.S. Growth, coenosarc pulsations, and hydroplasm movement in the colonial hydroid *Dynamena pumila* (L., 1758) placed in flow-through and nonflow cuvettes. *Biol. Bull. Rev.* **2019**, *9*, 52–61. [CrossRef]

51. Marfenin, N.N. Integration of a colony of the hydroid polyp *Dynamena pumila* (Hydrozoa, Leptolida). The reaction of the colony to freezing in winter. *Rep. Acad. Sci. USSR* **1971**, *199*, 489–492. (In Russian)
52. Marfenin, N.N.; Letunov, V.N. Some features of the feeding behavior of winter colonies of *Dynamena pumila* under various temperature conditions. *Biol. Sci.* **1980**, *1*, 51–56. (In Russian)
53. Kosevich, I.A. Mechanics of growth pulsations as the basis of growth and morphogenesis in colonial hydroids. *Russ. J. Dev. Biol.* **2006**, *37*, 90–101. [CrossRef]
54. Naumov, D.V. *Hydroids and Hydromedusae of the U.S.S.R (Keys to the Fauna of the USSR)*; Israel Program for Scientific Translations: Jerusalem, Israel, 1969; pp. 1–660.
55. World Sea Temperatures. 2023. Available online: https://www.seatemperature.org/ (accessed on 20 August 2023).
56. White Sea Water Temperature. 2023. Available online: https://seatemperature.net/seas/white-sea (accessed on 20 August 2023).