Available online at www.worldscientificnews.com

World Scientific News

An International Scientific Journal

WSN 160 (2021) 1-15 EISSN 2392-2192

Biology of reproduction of aquatic organisms: the course of oogenesis of freshwater jellyfish *Craspedacusta sowerbii* Lancester, 1880 in the Dnieper reservoir

Himchik Varvara, Marenkov Oleh*, Shmyhol Nadiia

Department of General Biology and Water Bioresources, Faculty of Biology and Ecology, Oles Honchar Dnipro National University, P.M.B. 49050, Dnipro, Ukraine

*E-mail address: gidrobions@gmail.com

ABSTRACT

Over the past few decades, the jellyfish *Craspedacusta sowerbii* Lancester, 1880 spread around the world, including the main waterway of Ukraine – the Dnieper River. It is known that invasive species can lead to serious changes in the ecosystems in which they fall. Therefore, studies of the biology and ecology of freshwater jellyfish in new reservoirs are relevant. The aim of the work was to determine the features of the oogenesis of jellyfish *C. sowerbii* Lancester, 1880, predict the population size next year, and assess the potential threats they may pose to the ecology of the Dnieper reservoir. Objectives of the study: to take samples of jellyfish in the Dnieper reservoir; perform histological sections of gametes of female jellyfish; to study the course of gametogenesis of jellyfish oocytes; determine the percentage of eggs ready for ovulation in the first generation of the breeding season; to establish the values of the nuclear-cytoplasmic ratio in jellyfish oocytes; to determine the peculiarities of reproduction of jellyfish of the species *C. sowerbii* Lancester, 1880; to predict the number of jellyfish of the next generations and to assess the possible consequences of the rapid reproduction and spread of this jellyfish on the ecosystem and fishery use of the Dnieper reservoir. The article states that there is a mass reproduction of jellyfish *C. sowerbii* Lancester, 1880 in the Dnieper reservoir that can lead to losses of fish products in 5740 t/year. After analyzing the histological sections of jellyfish, it was found that their reproduction is portioned, the share of mature eggs in the first generation is about 13 %. It was found that mature eggs have an area of 839.75 μm^2 and a diameter of 32 μm. It is estimated that next year we should expect an

(Received 01 July 2021; Accepted 22 July 2021; Date of Publication 23 July 2021)

increase in the population of jellyfish by almost 50 %. On the basis of the conducted researches the course of oogenesis of freshwater jellyfish in the conditions of the Dnieper reservoir is determined.

***Keywords*:** jellyfish, *Craspedacusta sowerbii*, the Dnieper Reservoir, oocytes, reproduction

1. INTRODUCTION

Invasions are one of the very serious problems of the modern living world. There are species that dramatically expand their range with the help of man or under the influence of his activities. Invasive organisms multiply rapidly and cause serious damage as they capture the ecosystem and dominate the local species. Invasion of non-native organisms is the second largest problem for biodiversity in the world after direct impact on habitat. Due to the fact that the effect of these organisms is not easy to notice, invasive hydroids are not given enough attention. Abroad, this jellyfish has been studied by many scientists such as Ernest Payne, Stanley Dodson, Ingrid Stradinger and many others, in Ukraine not many studies have been conducted, but D.V. Naumov, O.O. Protasov and N.E. Nikolaev did significant contribution to the study of this species [1]. One of the main species of stinging jellyfish – freshwater jellyfish *Craspedacusta sowerbii* Lankester, 1880 needed attention.

Recently, more and more jellyfish have appeared in the rivers of Ukraine and increased in number in the main waterway of the country – the Dnieper River [1, 2]. These freshwater jellyfish are invasive, which means not inherent in these waters. Similar scales of invasion can be compared with the spread of ragweed or Colorado potato beetle (*Leptinotarsa decemlineata*).

Currently, the impact of jellyfish on the ecology and biodiversity of aquatic ecosystems of Ukraine is not significant, due to the fact that the large level of distribution and reproduction of jellyfish was reached only in recent years. But if you do not pay attention to it now, in the future jellyfish can cause serious environmental and even economic problems associated with fish resources [4–7].

Massive eating of zooplankton by jellyfish and the fact that almost no one consumes this species of jellyfish can reduce the populations of zooplankton and even small fish over time, both by direct attack and accidentally, i.e. through contact with their stinging tentacles. Killed or eaten organisms are important trophic parts of the reservoir, as it is a closed waterbody, which means that these invasive jellyfish can disturb the natural order and adversely affect local species. Jellyfish can harm local species and change the structure of groups. By consuming large numbers of lower trophic organisms that feed on algae, these invasive jellyfish can also cause massive "blooming" of algae, which in turn negatively affects the state of freshwater systems.

Massive development of "bloom" of jellyfish can be significant and dense: 400 individuals/m^2. Due to the large "bloom", 13 % of the resources of otters can be consumed or killed by *C. sowerbii* Lankester, 1880 [6, 7]. Almost 10 % of populations of branched crustaceans (e.g. daphnia) are eaten daily by freshwater jellyfish [7]. The massive summer "bloom" of jellyfish could have a significant effect on fish eggs eaten by freshwater jellyfish. Currently, in the context of global warming, it is possible that the strong summer heat will contribute to the annual mass development of jellyfish [8].

The article presents the results of histological studies of the development of jellyfish eggs of *C. sowerbii* Lankester, 1880. The features of oogenesis defined by studying the nuclear-cytoplasmic ratio and the percentage distribution of mature and immature eggs of the first generation. Thus, we determined how many jellyfish give offspring in their lifetime, which further makes it possible to predict the number of this species.

2. BIOLOGY AND ECOLOGY OF JELLYFISH

Distribution of jellyfish. *Craspedacusta sowerbii* Lankester, 1880 – one of the first freshwater jellyfish known to scientists. It originates from the Yangtze River Basin in China, where it is found in both the upper and lower reaches of the river valley [2].

Freshwater jellyfish was first discovered in 1880 by scientists in the pool of the London Botanical Society, where it was introduced along with exotic plant species. Since *C. sowerbii* Lankester, 1880 do not know how to resist strong river flow, so they are most common in warm shallow, slow or stagnant water bodies, such as ornamental ponds, reservoirs, quarries, as well as in lakes, streams, ponds, rivers and even live in aquariums [9].

Their populations are growing rapidly around the world. They turned out to be the few species of animals that benefited from climate change [10–13]. Global warming has increased the areas suitable for them. In addition to warming, another reason for their spread is overfishing: after the loss of many species of rival predators, jellyfish received a rich forage base.

C. sowerbii Lankester, 1880 is considered a cosmopolitan species, the findings of which have been reported in many places on all continents except Antarctica. Its spread to all continents can be explained by the fact that with the ballast water of ships or on the bodies of fish or plants, aquarists transported several individuals in the late nineteenth century. Most people are inclined to believe that their spread is caused by the import of water lilies, to which jellyfish polyps were attached.

In Ukraine, this species was found in 1979 by Ukrainian professor Oleksandr Protasov in the reservoir of the Chornobyl NPP [1]. Jellyfish were then found in the Trypillya NPP, the Kaniv Reservoir and the Khmelnitsky NPP. But recently they can be seen in many parts of the country.

Systematic position of the species. The first taxonomic description of Craspedacusta dates back to 1880. Until 1938, the jellyfish was placed in the same order with Trachymedusae, although it has significant differences. A more precise systematics has now been adopted.

Domain: Eukaryotes
Kingdom: Animals (*Animalia*)
Subkingdom: *Eumetazoa*
Phylum: *Cnidaria*
Subphylum: *Medusozoa*
Class: *Hydrozoa*
Subclass: *Trachylinae*
Order: *Limnomedusae*
Family: *Olindiidae*
Genus: *Craspedacusta*
Species: *Craspedacusta sowerbii*

The generally accepted international scientific name is *Craspedacusta sowerbii* Lankester, 1880.

Morphological structure of jellyfish. *C. sowerbii* Lankester, 1880 has many similar features with most of jellyfish. It is a white or greenish gelatinous animal, which consists of 96.74% – 99.87% of water. Jellyfish do not have a head, skeleton, special organs for respiration or excretion [14].

C. sowerbii Lankester, 1880 is easiest to identify when it takes the form of a small domed jellyfish known as a hydromedusa. Hydromedusa is translucent, has a diameter of about 5–25 mm and weighs 3–5 grams. It has five opaque white channels that form the gastrointestinal cavity (four radial and one medial-sagittal or annular) and a wide annular muscle fold – the sail. The main difference between *C. sowerbii* Lankester, 1880 and the "real" scyphoid jellyfish is the presence of a vellum - a thin round membrane on the underside of the bell. From the center of the inner part of the dome hangs a large structure of the central stomach, called the manubrium, with an opening for the mouth, which consists of 4 lips. Four large flat genitals (gonads) are attached to the annular (radial) canal and are usually opaque white. The freshwater jellyfish has four very long tentacles, also called oral tentacles, each of which is parallel to the radial canal at the edge of the vellum (perradial tentacles). Shorter tentacles facilitate feeding, while longer tentacles provide stability during swimming and are arranged in several rows. The total number of tentacles ranges from 50 to 500 pcs. Each tentacle carries thousands of cnidocytes (stinging cells), and each cnidocyte has stinging capsules - nematocysts. Tentacles with nematocysts help to capture food and serve as a kind of protection against predators. They are used to detect light and darkness, providing another way to find food and avoid predators [14].

This organism can move at a speed of 0.1 m/s in any direction due to pulsating contractions on the surface of its dome. The edge of the socket consists of statocysts (sense organs that provide balance). While the veil consists of nematocysts, which are in sufficient numbers around the mouth. This is useful when the jellyfish grabs its prey, helping to draw it into the mouth of the jellyfish. *C. sowerbii* Lankester, 1880 – a predator that feeds on small organisms that come across it. Nematocysts are used by both polyps and jellyfish to capture prey.

Polyps consist of a head with nematocysts and an oral opening, behind which is a thin neck, as well as a root base, which is attached to a stationary substrate. They are able to disguise themselves by releasing sticky mucus that attaches the particles to their body. Polyps are often associated with the simplest, flatworms, small crustaceans, mites and insect larvae, and have been observed as symbionts on young striped perch.

Lifestyle. All stages of the life cycle of the jellyfish *C. sowerbii* Lankester, 1880 show a subtle relationship with environmental factors. The habitat of jellyfish should have a large rock surface so that polyps can attach. In addition, it is better if they are isolated from other rivers to limit the effects of cold water, which in turn limits the reproduction of *C. sowerbii* Lankester, 1880. Low temperature and high light intensity will allow water to reach +25 °C, which contributes to asexual and sexual reproduction of this jellyfish. An oxygen concentration above 0.26 mg/l is required for the survival of this jellyfish [15, 16].

According to researchers, the probability of encountering *C. sowerbii* Lankester, 1880 increases in freshwater, mainly due to climate change: a warmer and longer summer will contribute to the spread of jellyfish [17]. Freshwater jellyfish can be found in the summer and autumn months, with August and September being the peak months. They are more active during the day, at other times jellyfish tend to lie on the bottom of shallow water, storing their energy to find food.

Elevated water temperature and a sufficient number of forage organisms contribute to the reproduction of this species. Polyps are usually found in an aqueous medium that is more oligotrophic than eutotrophic. Large flows most often cause damage and disintegration of polyps. The polyp is found mainly in natural alkaline environments, such as flooded gravel quarries, limestone quarries or cement pools. The findings of *C. sowerbii* Lankester, 1880 in swampy waters were not reported, so, most likely, the jellyfish can not live in acidic conditions [18].

Jellyfish are sensitive to fluctuations in osmotic pressure. Survival time decreases with increasing osmotic pressure. The peak survival time of 200 hours was recorded at 0.2 mosm/l. Polyps exist in the temperature range from +4ºC to +33ºC, the optimal temperature for their growth and development is +19–25ºC (Table 1).Younger organisms need a higher water temperature to grow. The most favorable for the reproduction of jellyfish are shallow waters, well-heated, with a weak current and usually the reproduction of jellyfish occurs in summer and autumn. Higher turbidity or increased intensity of "blooming" of water provides more favorable conditions for the emergence of free-swimming individuals of this species of jellyfish. There is a nonlinear relationship between population density and lifetime. It was found that the lower the population density, the larger the individuals.

Table 1. Conditions for the existence of freshwater jellyfish.

Environment parameters	**Indicator**	**Characteristic**
Minimal temperature (ºC)	+4	At temperetures below +4 ºC in the laborarories – the animals died.
Maximal temperature (ºC)	+33	At maximum temperature in culture abnormal reproduction of polyps are observed.
Minimal water salinity (‰)	0	*C. sowerbii* can be found in lakes, streams, ponds, rivers.
Maximal water salinity (‰)	3	Jellyfish started to settle in laboratories.
Minimal value of pH	6.7	Jellyfish and polyps were noticed in ponds with pH levels between 6.7–8.4, but are absent in the furthest pond with pH levels between 8.5–9.7. But the role of pH levels in jellyfish reproducture is not understood yet.
Maximal value of pH	9.7	
Minimal reproductive temperature (ºC)	+15	Reproductive temperature for jellyfish
Maximal reproductive temperature (ºC)	+33	
Climate		Cool temperate-subtropical

Sexual reproduction of jellyfish lasts about 22 days. The number of newly formed polyps and jellyfish strongly depends on the population density. That is, the greater the density of polyps, the more free-

floating jellyfish are formed, and the more free-living jellyfish - the more polyps they form during reproduction.

Feeding. *C. sowerbii Lankester*, 1880 – a predator that feeds on small organisms that come across it. Freshwater jellyfish are mostly not eaten by fish, but are known to prey on two species of fish (*Crassius sp., Lebistes sp.*) and two species of crayfish (*Orconectes rusticus, Orconectes propinquis*), but it can sting these aquatic organisms, which sometimes causes necrosis of their tissues. An experiment conducted in northern Italy showed that jellyfish *C. sowerbii* Lankester, 1880 feed on zooplankton, preferring a complex of species of daphnia, cyclops, cladocer sizes from 0.1 to 3 mm. But the polyps of this freshwater jellyfish feed on a wide range of small victims: larvae of nauplii, rotifers, crustaceans, nematodes and insects. There is evidence that jellyfish can feed on caviar and fish larvae [19, 20].

When *searching* for food, jellyfish descend from the surface into deeper layers of the aquatic environment. The average digestion time is 4-5 hours. The largest amount of prey in the gastric cavity of freshwater jellyfish is found at night, on average, jellyfish can consume up to 10 % of their body weight.

Life cycle. Freshwater jellyfish are dimorphic, *alternating* both asexual generation (benthos polyp) and sexual generation (jellyfish morph). Mature jellyfish reproduce sexually, throwing gametes into the water, i.e. external fertilization, parthenogenesis is not detected. Fertilized eggs turn into ciliated larvae – motile larvae, which in shape and size resemble a ciliate shoe, they move in search of a suitable substrate, which settles to the bottom, attaching to the substrate (stones, aquatic plants, etc.) and form polyps. The newly formed polyp is only 0.3 mm long. However, sexual reproduction is very rare, because populations of *C. sowerbii* Lankester, 1880 are often same-sex, consisting of either females or males. The life cycle of *C. sowerbii* Lankester, 1880 belongs to the metagenetic intestinal, the main part of their life cycle is the generation of polyps. Craspedacusta polyps are solitary or can form colonies [21, 22].

The life stage of polyps is quite hardy, it is able to adapt to a wide range of temperatures, and under adverse conditions it is able to form podocysts, which are dormant cell layers surrounded by a chitinous membrane (periderm), which allows them to withstand more extreme conditions than active forms. It happens like this: under adverse conditions, the polyp can regress and form a body at rest. The polyp is compressed into a solid mass, and goes into an inactive state. Podocyst in its purpose is very similar to cysts in microorganisms and can survive in drought conditions for about 40 years, while maintaining its viability. Under favorable conditions, podocysts again turn into polyps.

Polyps grow and can form three types of buds:

1) Daughters polyps that remain attached to the parent polyps. They form colonies consisting of two to seven individuals ranging in size from 5 to 15 mm and they are devoid of tentacles.
2) Buds that are able to produce larvae (asexual reproduction), the so-called frustula, devoid of the mouth, they move to new places before turning into new polyps.
3) Under favorable conditions, when the water temperature exceeds +20 ºC for a long time, polyps form special buds, from which a free-floating jellyfish emerges [23].

An adult appears only under certain favorable conditions, under other conditions the jellyfish can exist for many seasons in the form of a polyp. This feature explains the unexpected appearance of a large number of freshwater jellyfish in any body of water.

The formation of jellyfish occurs by lateral budding of polyps. Fernandus Payne described the early development after gametes and fertilization. The full life cycle from egg to pelagic free jellyfish lasts from 34 to 51 days [14]. The zygote has one equal division, all subsequent divisions are unequal. The zygote turns into a flickering free-floating blastula, then the segmentation cavity is filled with endodermal cells. After some time after that, the whole structure lengthens and forms the inner gastric cavity. Attachment occurs at one end, the mouth and nematocysts open, and a typical polyp forms. The body shape of a freshly budded jellyfish (about 1 mm in diameter) is close to a spherical one. During development, the shape changes and takes the form of a flattened hemisphere with a diameter of up to 20 mm. In addition, during development, the number of tentacles increases (from 16 to 500 pcs.) and the balance organs – statocysts are laid down. The formation of jellyfish is intermittent, between "flowering" can take several years [22–24].

3. MATERIALS AND METHODS

The basis of the study is study our own research materials about jellyfish in the water area of the Dnipro River in summer of 2020 (Fig. 1). The hydrobiological material was selected at monitoring station located in the Dnieper Reservoir (near Stary Kodaky village 48º22′45″N, 35º07′59″E).

Figure 1. Sampling points.

Collection of free-floating individuals was performed with a net, manually and with the help of plankton mesh in accordance with generally accepted hydrobiological methods [25].

Collected jellyfish had gonads at different stages of development. The number of jellyfish was calculated using a hydrobiological framework 1×1 m.

Histological methods of research were used to study the jellyfish oocytes. Jellyfish were fixed in a 4% formalin solution with further processing after conventional histological methods [26]. Sections were made using microtome "Thermo Fisher Scientific NM 355S". Histological sections were stained with hematoxylin-eosin.

Photographs of the preparations were made using a digital camera for the microscope "Sciencelab T 500 5.17 M", connected to the microscope ULAB Infinite Plan Achromatic XY-B2T Led (Fig. 2). 100 microscope oocytes were analyzed and measured. Histological sections were described using histology atlases [27–29].

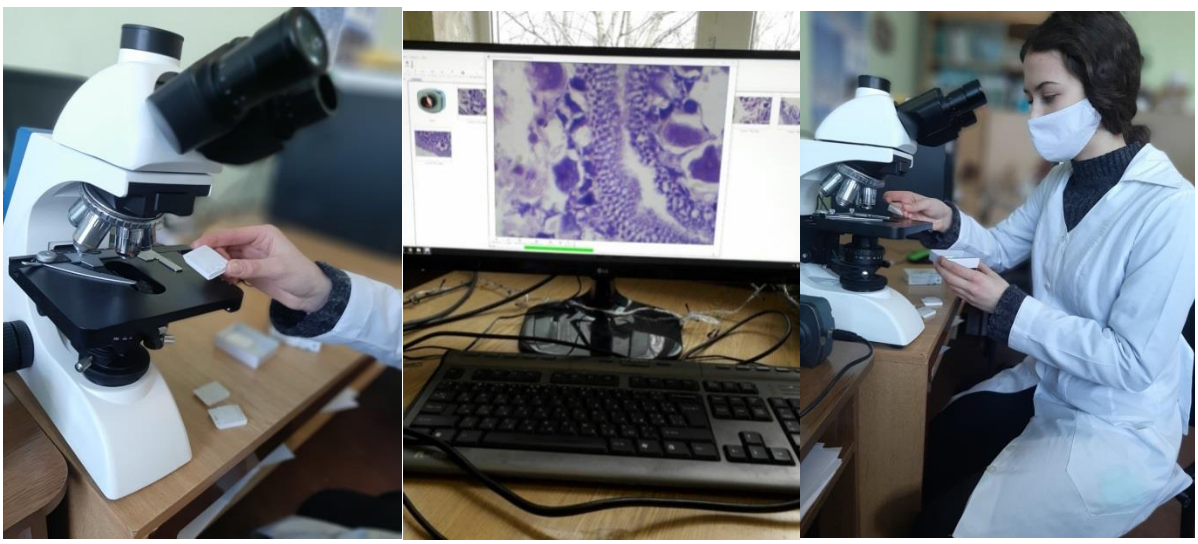

Figure 2. Photos of the research process.

The nuclear-cytoplasmic ratio (NC ratio) was calculated as the ratio of the area of the cell nucleus to the area of the cytoplasm [30]. The data was statistically processed according to standard methods using the software package Statistica 8 .0 (StatSoft Inc., USA). All results are presented as the mean ± standard deviation (SD). The significance of differences between the data samples is determined by one-way ANOVA test with a significance level of $p<0.05$. Bioethical norms were not violated during the research.

4. RESULTS AND DISCUSSION

The number and biomass of jellyfish and their impact on the bioproductivity of the ecosystem. At a water temperature of +25 °C in the Dnieper reservoir near the village Stary Kodaky there was a mass development of freshwater jellyfish *C. sowerbii* Lankester, 1880 (Fig. 3). The number of individuals averaged 10 specimens / 1 m^2. With an average weight of jellyfish of 3.5 g, the biomass of jellyfish during mass development was about 35 ± 0.5 g / 1 m^2 of water.

Figure 3. Collected samples of jellyfish.

Most jellyfish *C. sowerbyii* feed on zooplankton, preferring a complex of species of daphnia and cyclops from 0.1 to 3 mm. Given that the diet of jellyfish can average about 10 % of the mass per day, freshwater jellyfish consume about 0.35 g of zooplankton per day. Given the number and biomass of jellyfish per 1 m^2 of reservoir – 10 specimens, it can be estimated that jellyfish consumes 3.5 g of zooplankton per 1 m^2 in the summer, which can be 1435 tons of zooplankton per day in terms of the total area of the Dnieper Reservoir (410 km^2). Given the feed ratio of zooplankton – this corresponds to 287 tons of potential fish production per day. Considering the average lifespan of freshwater jellyfish – 20 days – the amount of damage to fish products due to the loss of zooplankton can reach 5740 tons.

Histological picture of the initial stages of oocyte development. The smallest oocytes were found in individuals of the juvenile stage, at the stage of development of a single-layer follicle C. Oocytes had a diameter of 4.5 to 8 μm, – small basophilic cells with a homogeneous cytoplasm. In the studied jellyfish eggs, the nucleus, which occupied the central position and reached an average diameter of 0.8±0.15 μm, was clearly traced.

Due to the continuous process of reproduction during the stage of free-floating jellyfish, asynchronous development of germ cells was observed. The cells of the early stages of gametogenesis are presented – single-layer follicles and cells of later stages of development: phases D and E (Fig. 4).

Oocytes of different periods and phases of development are visible on the histological section (Fig. 6). Noticeable oocytes that form several generations. Noticeable large oocytes in the phase filled with yolk (E), larger ones form the first portion of eggs, oocytes in the phase of the beginning of yolk accumulation (D), they are smaller in size and, obviously, form the next portion of eggs. In addition to these generations of oocytes in the monads there are oocytes in the initial phases of vacuolation and a complex of oocytes of the period of protoplasmic growth.

Figure 4. Asynchronous development of jellyfish oocytes, magnification 200x.

Morphological analysis of jellyfish gonads. To study the reproductive potential of jellyfish, we measured the area of freshwater jellyfish eggs through a special program TSView7 and manually selected each egg (Fig. 5), mostly selected more mature eggs with clear edges. The program, after calibration, automatically made calculations S, expressed in μm^2.

Table 2. Cytological examination of jellyfish oocytes.

Indicators, n = 50	Admeasurement
The area of oocytes in phase E, μm^2	839.75±21.45
The area of nuclear oocytes in phase E, μm^2	109.09±12.43
The area of oocytes in phase D, μm^2	85.12±4.12
The value of the NC ratio for oocytes of phase E	0.13

Observed the uneven development of oocytes, which indicates the portion reproduction of jellyfish. This promotes constant reproduction, in favorable conditions during the growing season. Mature eggs of phase E had an area of 839.75 μm^2, and the diameter of mature eggs reached about 32 μm. Immature phase D eggs were almost 10 times smaller and were in the phase of cytoplasmic growth, so for their maturation requires nutrients that the jellyfish will receive as a result of nutrition. The NC ratio for mature eggs was 0.13 units, which indicated the readiness of the eggs for spawning. Under favorable conditions, these eggs mature and form the next generation of offspring (Table 2).

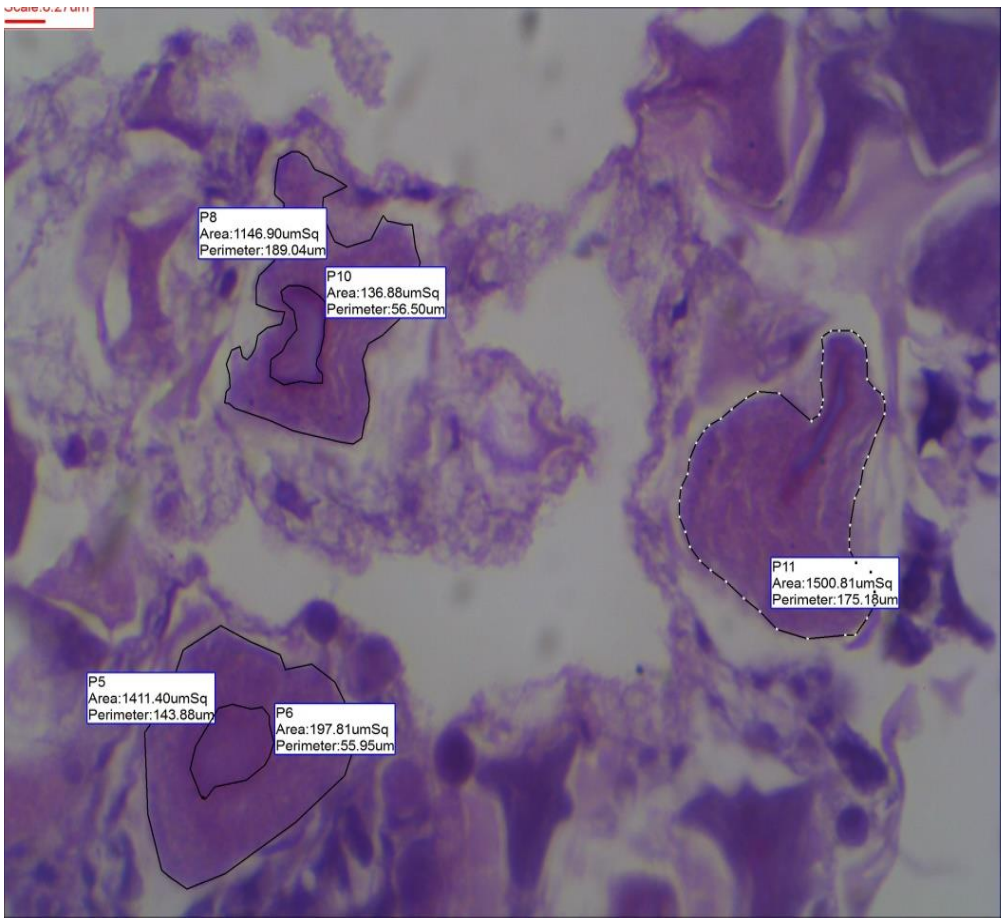

Figure 5. Cytological measurements of cell and nucleus areas using TSView7, magnification 400x.

Histological picture of oocyte maturation of freshwater jellyfish. Mature oocytes are rather small cells with a homogeneous cytoplasm, a clear central nucleus. Oocytes are located in the follicular membrane. We observed small depths of the yolk in the cytoplasm, which are located over the entire area of the ovum (Fig. 6).

In the phase of filling the oocyte with yolk (phase E), the yolk granules are placed over the entire area of the oocyte from the shell to the nucleus. The lumps of the yolk are oval or rounded. In phase E oocytes, the yolk filled the entire oocyte and formed well-marked lumps, creating a homogeneous mass. At this stage, the eggs are fully formed. This is followed by spawning the eggs. Jellyfish oocyte yolk plays an important role in egg development. When oocytes mature, the yolk granules fill the entire cytoplasm of the cell. The depths of the yolk have a rounded shape and are characterized by weak eosinophilia. Upon completion of oogenesis, the yolk granules merge into large droplets. The ratio of immature eggs to mature was 7 : 1 (Fig. 7).

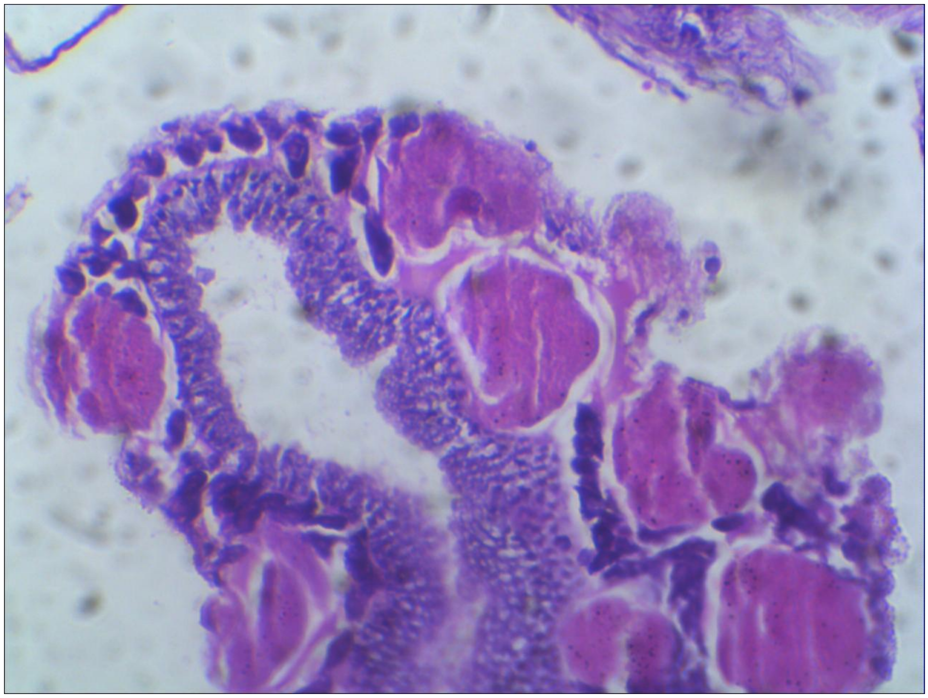

Figure 6. Mature oocytes of freshwater jellyfish, magnification 200x.

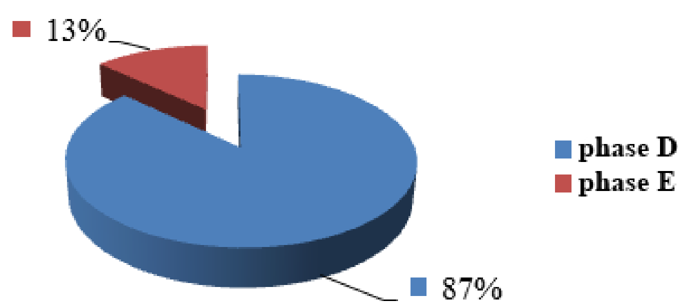

Figure 7. The ratio of different groups of jellyfish oocytes.

The individual fertility of jellyfish was calculated by directly counting the number of oocytes in histological sections of jellyfish and averaged was 457.5 ± 23.1 eggs, with working fertility, the number of eggs that mature in the first generation accounted for 13 %, i.e. about 59 eggs. Thus, one jellyfish in the first generation gives 59 mature eggs, based on the fact that 1 m^2 accounted for about 10 specimens of jellyfish, so they could give 590 eggs in the first generation. The frequency of spawning jellyfish under favorable conditions can reach 5 times, i.e. it can lay the mature eggs 5 times. Thus, the number of laid eggs increases to 2950 eggs, which can potentially form polyps, even with the lowest survival rates of eggs (planulas and young polyps) at the rate of 0.001%, can potentially form 2.9 (rounding up to 3) polyps. Each of the polyps can form from 5 to 10 free-floating jellyfish, if you take into account the minimum number of 5 free jellyfish. Then the next year from 3 polyps it can form 15 mature jellyfish, which can increase the population of jellyfish by almost 50 %.

5. CONCLUSIONS

1) At a water temperature of +25 °C in the Dnieper Reservoir there was a mass development of freshwater jellyfish *C. sowerbii* Lancester, 1880. The number of jellyfish in the summer averaged 10 specimens per 1 m^2. It is estimated that the amount of damage to fish products due to the loss of zooplankton can reach 5740 t / year.
2) The smallest oocytes were found in individuals of the juvenile stage, at the stage of development of a single-layer follicle C. Oocytes this stage had a diameter of 4.5 to 8 μm.
3) Observed the uneven development of oocytes, which indicates the portioned reproduction of jellyfish. This promotes constant reproduction, in favorable conditions during the growing season. Mature eggs of phase E had an area of 839.75 ± 21.45 μm^2, and the diameter of mature eggs reached about 32 ± 1.22 μm. Immature eggs of phase D were almost 10 times smaller and were in the phase of cytoplasmic growth.
4) The individual fertility of jellyfish averaged 457.5 ± 23.1 eggs, with working fertility, the number of eggs that mature in the first generation accounted for 13 %, i.e. approximately 59 eggs. According to our forecasts, the population of jellyfish may grow by almost 50 % next year, which will lead to even greater losses.
5) On the basis of the conducted researches the idea of the course of gametogenesis of freshwater jellyfish in the conditions of the Dnieper reservoir is expanded. Determining the phases of development of freshwater jellyfish oocytes is of great theoretical and practical importance, as understanding the processes of jellyfish reproduction in the Dnieper will allow to develop comprehensive measures to predict their spread by water bodies in Europe.

Referenses

[1] Protasov, A. A., Starodub, K. D., & Afanas' ev, S. A. (1981). A polyp of Craspedacusta sowerbii in the cooling reservoir of Chernobyl' Nuclear power station Ukrainian-SSR. *Vestnik Zoologii*, 15, 67-68

[2] Yakovenko V. O. & Fedonenko O. V. (2021) Invasion of jellyfish Craspedacusta sowerbii Lankester, 1880 in the Zaporozskoe reservoir. *Problems of Ecology and Nature Protection of the Nechnogenic Region*, 12, 195-200

[3] Oualid, J. A., Iazza, B., Tamsouri, N. M., El Aamri, F., Moukrim, A., & López–González, P. J. (2019). Hidden diversity under morphology–based identifications of widespread invasive species: the case of the 'well–known'hydromedusa *Craspedacusta sowerbii* Lankester 1880. *Animal Biodiversity and Conservation*, 42(2), 301-316

[4] Hroudova, M., Vojta, P., Strnad, H., Krejcik, Z., Ridl, J., Paces, J., & Paces, V. (2012). Diversity, phylogeny and expression patterns of Pou and Six homeodomain transcription factors in hydrozoan jellyfish Craspedacusta sowerbyi. *PLoS One,* 7(4), e36420

[5] Dodson, S. I., & Cooper, S. D. (1983). Trophic relationships of the freshwater jellyfish *Craspedacusta sowerbyi* Lankester 1880. *Limnology and Oceanography*, 28(2), 345-351.

[6] Stadel, O. (1961). Neuere Kenntnisse über Ökologie und Verbreitung der Süßwassermeduse Craspedacusta sowerbii. *Abh. Verh. Naturwiss. Ver. Hamburg*, 5, 157-192

[7] Delaney, D. G., Sperling, C. D., Adams, C. S., & Leung, B. (2008). Marine invasive species: validation of citizen science and implications for national monitoring networks. *Biological Invasions*, 10(1), 117-128

[8] Silva, W. M., & Roche, K. F. (2007). Occurrence of the freshwater jellyfish *Craspedacusta sowerbii* (Lankester, 1880) (Hydrozoa, Limnomedusae) in a calcareous lake in Mato Grosso do Sul, Brazil. *Biota Neotropica*, 7(1), https://doi.org/10.1590/S1676-06032007000100028

[9] Smith, A. S., & Alexander Jr, J. E. (2008). Potential effects of the freshwater jellyfish *Craspedacusta sowerbii* on zooplankton community abundance. *Journal of Plankton Research*, 30(12), 1323-1327

[10] Fuentes, R., Cárdenas, L., Abarzua, A., & Caputo, L. (2019). Southward invasion of Craspedacusta sowerbii across mesotrophic lakes in Chile: geographical distribution and genetic diversity of the medusa phase. *Freshwater Science*, 38(1), 193-202

[11] Lüskow, F., López-González, P. J., & Pakhomov, E. A. (2021). Freshwater jellyfish in northern temperate lakes: Craspedacusta sowerbii in British Columbia, Canada. *Aquatic Biology*, 30, 69-84

[12] Teubner, K., Großschartner, M., & Teubner, I. E. (2018). Response of zooplankton to restoration and climate warming in Alte Donau. In *The Alte Donau: Successful Restoration and Sustainable Management* (pp. 163-212). Springer, Cham.

[13] Akbar, N. A., & Ali, L. A. (2020). A Study of Zooplankton Community in Alwand River and Dam-Iraq. *Zanco Journal of Pure and Applied Sciences*, 32(3), 116-126

[14] Payne, F. (1924). A study of the fresh-water medusa, Craspedacusta ryderi. *Journal of Morphology,* 38(3), 387-429

[15] Spadinger, R., & Maier, G. (1999). Prey selection and diel feeding of the freshwater jellyfish, *Craspedacusta sowerbyi*. Freshwater Biology, 41(3), 567-573.

[16] Gershwin, L. A. (2016). Chapter two. jellyfish life history. In *Jellyfish* (pp. 54-93). University of Chicago Press.

[17] Larambergue (de) M. (1945). Remarques sur la biologie de *Craspedacusta sowerbyi* Lank. à propos de l'apparition de Méduses dans un aquarium à Lyon. *Bull Soc Linn Lyon* 14(2): 13-18

[18] Acker, T. S., & Muscat, A. M. (1976). The ecology of *Craspedacusta sowerbii* Lankester, a freshwater hydrozoan. *American Midland Naturalist*, 323-336.

[19] Kozuharov, D., Kalchev, R., Beshkova, M., Stanachkova, M., Kenderov, L., Vasilev, V., & Trichkova, T. (2017). Occurrence of the alien freshwater jellyfish Craspedacusta sowerbii Lankester, 1880 (Cnidaria: Hydrozoa) in some Bulgarian reservoirs. *Acta Zoologica Bulgarica*, (Supplementum 9), 67-72

[20] Riyas, A., & Kumar, A. B. (2017). Record of freshwater jellyfish blooms of invasive Craspedacusta sowerbii Lankester, 1880 (Hydrozoa, Limnomedusae) from Kerala, India. *Journal of Aquatic Biology*, *Fisheries*, 5, 154-159.

[21] Kęstutis Arbačiauskas, Jūratė Lesutienė. (2005) The Freshwater Jellyfish (*Craspedacusta sowerbii*) in Lithuanian Waters. *Acta Zoologica Lituanica* 15, 1, 54-57

[22] Karaouzas, I., Zogaris, S., Lopes-Lima, M., Froufe, E., Varandas, S., Teixeira, A., & Sousa, R. (2015). First record of the freshwater jellyfish Craspedacusta sowerbii Lankester, 1880 in Greece suggests distinct European invasion events. *Limnology*, 16(3), 171-177.

[23] Stanković, I., & Ternjej, I. (2010). New ecological insight on two invasive species: Craspedacusta sowerbii (Coelenterata: Limnomedusae) and Dreissenia polymorpha (Bivalvia: Dreissenidae). *Journal of Natural History*, 44(45-46), 2707-2713

[24] Jankowski, T. (2000). Chemical composition and biomass parameters of a population of Craspedacusta sowerbii Lank1880 (Cnidaria: Limnomedusa). *Journal of plankton research*, 22(7), 1329-1340

[25] Arsan, O.M., Davydov O.A., Dyachenko T.M., Yevtushenko N. Yu. Zhukinskiy V. M., Kirpenko N.I. & Kipnis L.S. (2006). Metody gidroekologichnykh doslidzhen poverkhnevykh vod. (Methods of hydroecological investigations of surface waters.) Kyiv, Logos Press.

[26] Shields, J. D. & Boyd, R (2014). Atlas of Lobster Anatomy and Histology, Virginia Institute of Marine Science, Gloucester Point.

[27] Lőw, P., Molnár, K., & Kriska, G. (2016). Atlas of animal anatomy and histology. Springer.

[28] Marenkov, O., Lykholat, T., Kurchenko, V., & Nesterenko, O. (2018). Histology of marbled crayfish Procambarus virginalis (Lyko, 2017): annotated atlas. *World News of Natural Sciences*, 21, 141-153

[29] Marenkov, O., Fedonenko, E., Ananieva, T., & Tarnopolskaya, D. (2017). Annotated histological atlas (normal histology). *World Scientific News*, 90, 101-126.

[30] Nivia, M., Sunil, S. N., Rathy, R., & Anilkumar, T. V. (2015). Comparative cytomorphometric analysis of oral mucosal cells in normal, tobacco users, oral leukoplakia and oral squamous cell carcinoma. *Journal of Cytology*, 32(4), 253–260. https://doi.org/10.4103/0970-9371.171241