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Bioluminescence Characteristics Changeability of Ctenophore *Beroe ovata* Mayer, 1912 (Beroida) in Ontogenesis

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Abstract

The changes of the biophysical characteristics of light-emission in ontogenesis of ctenophore *Beroe ovata* Mayer, 1912 – recent introducer to the Black Sea has been researched. It is established, that bioluminescent amplitude of larvae was eight times higher, and energy of light-emission seven times more, than similar parameters of the bioluminescence in eggs of ctenophores. Amplitude and energy of light-emission of quite recently caught ctenophore (in control) were some orders more than similar parameters in ctenophores after spawning.

The maximum bioluminescent amplitude values were observed in the group of ctenophores with eggs-laying. It was registered a significant increase of light-emission characteristics of ctenophores with increasing body. Substantiated conclusion, that distinctions in the bioluminescence parameters of ctenophores in ontogenesis can be caused by ontogenetic features of their biochemical structure and quantity involved in bioluminescent reaction photocytes.

Keywords: Light-emission parameters, *Beroe ovata*, life cycles, Black Sea

Introduction

Ctenophores *Mnemiopsis leidyi* A. Agassiz, 1865 and *Beroe ovata* Mayer, 1912, invaded the Black Sea in 80-90-ties of the past century, effected considerably on the Black Sea ecosystem. Ctenophore *M. leidyi* invaded the Black Sea aquatorium with the ballast waters in the end of 80-ties. The mass growth of *M. leidyi* abundance was noticed beginning from 90-ties (Mutlu, 1999). This alien-species affected the feed mezozooplankton biomass, having undermined feed base of the plankton-eating fish-the base of the Black Sea market, pelagic fishes: anchovy, sprat, scad (Gucu, 2002) considerably, together with another factors (climatic changes, in particular).

Thus, ctenophore *M. leidyi* invasion deformed trophic links and sharply decreased abundance of mezozooplankton, including copepoda *Calanus euxinus*-the important component of the pelagic fish food (Gubanova, 2003). Mass growth of *M. leidyi* caused increase of the fish larvae share with the empty stomachs, which led to the food fish population decrease and their catches reduction more than 5 times by 1991 (Gordina *et al*., 2005), resulted in economy loses because of the anchovy stocks decrease, evaluated in 240 million dollars per year (Zaitsev and Ozturk, 2001).

Another ctenophore *B. ovata*, which eats mnemiopsis, invaded the Black Sea at the end of 90-ties. *Mnemiopsis* abundance had been decreased by 2000-2001, because *B. ovata* grazed *M. leidyi* and that improved the nutritive base of plankton-eating fish and their larvae state (Gordina *et al*., 2005). Many ecology-physiological characteristics of ctenophores *B. ovata* are well-studied because they play a very important ecological role in the Black Sea ecosystem (Finenko *et al*., 2006; Shiganova *et al*., 2001; Shushkina *et al*., 2000).

A special attention is given to *B. ovata* growth, development and reproduction, as this hydrobiont controls *M. leidyi* abundance (Anninsky *et al*., 2007; Arashkevich *et al*., 2001; Zaika, 2005). There are a sufficient number of literature included extensive lists of investigations of bioluminescence reaction irritation processes (Haddock *et al*., 2010), bioluminescence mechanisms of different organisms (Lapota, 2012; Shannon, 2002), light-emission daily rhythmic (Harvey, 1952), stimulation types (Haddock *et al*., 2010; Lapota, 2012) and bioluminescence organisms spectral characteristics (Hastings, 1995; Herring, 1990). Though, bioluminescence of *B. ovata*, as general representative of the Black Sea light-emission macroplankton, is not well-studied. Particularly, before now it was not being known the

change ways of organism's light-emission parameters in its growth, ontogenesis and reproduction state, what was the purpose of this research.

Materials and Methods

The investigation of *B. ovata* bioluminescence parameters in ontogenesis was carried out in Department of Biophysical Ecology of the Institute of Biology of the Southern Seas NAN Ukraine in September-November 2007-2008. *B. ovata* ctenophores were caught by Jedy net in the layer of 0-50 m in the Sevastopol coastal zone with removal from the shore up to 2 miles. The *B. ovata* luminescence parameters were registered using the laboratory complex "Light" by methods of mechanical and chemical stimulation (Tokarev *et al*., 2008). Three experiment series were conducted: 1) depending on ctenophore size (body length and mass); 2) depending on their physiological state and 3) on ontogeny stage. Uniform-sized group of *B. ovata* individuals with wet weight from 0.06 to 19.53 g was selected for the first experiment series. Just-caught unbroken individuals were placed into containers (3-5 liter) with filtered marine water (membrane filters pore diameter is 35 μm) at a temperature of 21±2°C, where they were adapted to experiment conditions during 2 hours.

For the purpose of measure bioluminescent biophysical characteristics variability of *B. ovata* in relation to reproduction stage organisms were divided into four groups: 1) individuals 50-mm long in the period before gonada formation-just-caught from sea, but adapted to experiment conditions in total darkness during two hours in order to avoid photoinhibition; 2) individuals 50-mm long with mature gonads, which were appeared as the experiment feeding result; 3) ctenophore eggs spawned by the second group; 4) ctenophore larvae grown from eggs of the third group.

Mature just-caught *Beroe* individuals (L=50 mm) in order to egg obtainment were placed singly in containers (18-20 liter) with filtered water under temperature 21±2°C and their were feeding with *M. leidyi* (L=35-40mm). Eggs calculation was carried out by the methodology (Arashkevich *et al*., 2001). The next day water from the containers was poured off through a syphon with 100 μm sieve cells, previously selected post-spawning individuals. During the first discharge 300-500 ml of water were left in the containers, then the containers were filled with filtered water again and all the procedure was repeated. The eggs collected on the mesh were washed off into a 200-ml glass and calculated under the binocular, in relation of eggs' quantity it was about 1/3-1/10 parts of a sample. The experiments were conducted upon scattered illumination; the temperature was according to *in-situ* conditions. Tested organisms' sizes were measured with a ruler directly in the experimental containers. Body volume was measured after the experiment procedure by the methodology of water replacement from a graduated cylinder. *M. leidyi* body volumes (for *Beroe* feeding) were obtained by equation, which connects ctenophore length with its volume (Arashkevich *et al*., 2001). Fixed number of just-spawned eggs (100-300 ind.) was put into 100-ml containers with round bottom. Eggs from one part of each container were taken for further bioluminescent signal's registration. Every day the containers were tested under the binocular, noting egg's degree of development. The other part of eggs in the containers was selected, and hatched larvae were taken and counted from it. Then, the larvae were stimulated singly for investigation of bioluminescent signals' characteristics. Experiments of *B. ovata* light signal registration by ontogeny stages were begun after adaptation period (two hours). *B. ovata* bioluminescent characteristics were compared before, during and after spawning for the purpose of estimating the reproductive function influence on organism's physiological state and bioluminescent signals values.

Results

Light-emission energy indicators definitely depend on quantity of secret, which is produced in a moment of irritation the animal. The more the age and therefore the linear dimension and body mass growth, so the more is the secret content. Consequently, light-emission amplitude is a function of organism's mass. Amplitude and bioluminescent signal duration of newly-caught ctenophores directly depend on dimension, i. e. on wet weight of the investigated organism (Figure 1).

Thus, light-emission intensity of *B. ovata* first size group (body mass 0.06±0.003 g) under mechanical stimulation was two times more than the one under chemical stimulation, achieved $(11.39\pm0.56)\cdot10^8$ quantum$\cdot s^{-1}\cdot cm^{-2}$. Bioluminescent amplitude rose when ctenophore body mass had increased from 0.06 to 19.53 g, achieving $(925.74\pm45.27)\cdot10^8$ quantum$\cdot s^{-1}\cdot cm^{-2}$. The shortest bioluminescent signals (0.94 s-under mechanical and 0.46 s-under chemical stimulation) were produced by small-sizes ctenophores. Ctenophore bioluminescent signal duration enhanced, achieving from 1.44 to 2.37 s, as body mass rises.

Signal durations of the largest individuals with medium body mass of 19.53±0.97 g were under the both stimulation types maximum and reached 3.79±0.17 s, being 2-2.5 times more, than small-sized individuals produce.

Caught from the sea ctenophores *B. ovata* (length 45-50 mm) were divided into three groups in order to investigate ctenophore reproduction system state's influence on their bioluminescent characteristics. The first group was composed by just-caught ctenophores with gonads at early development stages. This group served as a control and produced bioluminescence after two-hour adaptation in filtered

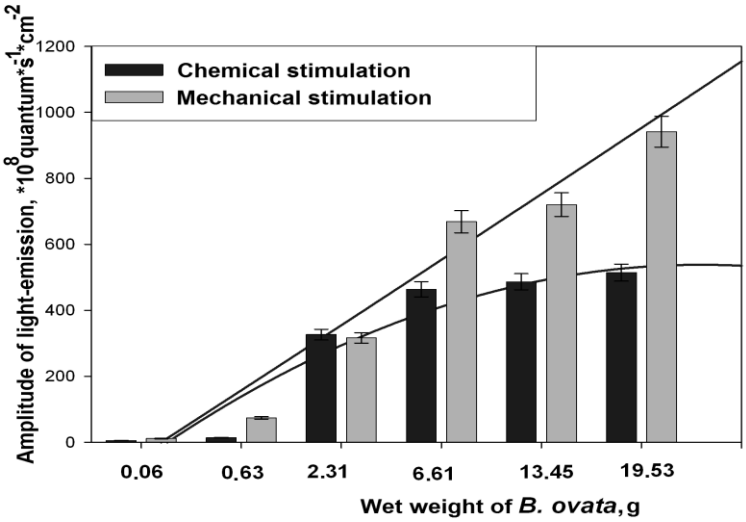

Figure 1. *B. ovata* light-emission amplitude in terms of organism wet weight under mechanical and chemical stimulation.

water. The second group included ctenophores with eggs clutches appeared in laboratory after experimental feeding. Individuals from this group before bioluminescent characteristics measurement were kept during 5 hours in 5-liter containers, where one *Mnemiopsis* (length 35-40 mm) was placed per one *Beroe*. Eggs clutches were ready for spawning in 1-2 days after feeding. The second group was tested after their eggs clutches had formed.

The third *Beroe* group included post-spawning individuals. These ctenophores were previously exposed in conditions similar to the second group had before clutches appearance. Ctenophore bioluminescent characteristics of the third group were registered immediately after spawning. The experiment results revealed that light signal amplitudes were maximum in the second group (with egg clutches), being 2-3 times more ($P<0.05$) than in the control group (just-caught individuals) (Figure 2).

But comparison of bioluminescent signal amplitude in the control group and in the post-spawning group detected that this value was three times more in the control group under mechanical stimulation and four times more under chemical stimulation.

Bioluminescent energy of spawning ctenophores with eggs clutches achieved maximum values, comparing with other groups $(434.41\pm21.7)\cdot10^8$ quantum$\cdot$cm^{-2}. It was two times more than in the control group, where bioluminescent energy was $216.15\cdot10^8$ quantum$\cdot$cm^{-2}, seven times more ($P<0.05$) in post-spawning group under mechanical stimulation and four times more-under chemical stimulation. The lowest energy values $(56.77\pm2.83)\cdot10^8$ quantum$\cdot$cm^{-2} were registered in the post-spawning group.

Bioluminescent signal durations in the second group (with eggs clutches) were similar to the control group, being equal to 2.27 and 2.49 s respectively. However, it was 1.5 times more than in the post-spawned group, which had the lowest light-emission time-up to 1.51±0.07 s.

Beroe with body length of 50 mm nourished after experiment with *Mnemiopsis* spawned on the very first day. The other part spawned for the experimental second day, i. e. in 2-3 days after food digestion. The clutch contained from 2.0 till 7.0 thousands of eggs with size up to 0.80-0.85 mm. Free-swimming larvae with body length of 0.4-0.5 mm appeared on the third day after spawning.

Beroe eggs had poor bioluminescence, expressed in low amplitude peaks-up to $(0.76\pm0.03)\cdot10^8$ quantum$\cdot$s$^{-1}\cdot$cm^{-2}, in low-level bioluminescent energy parameters-up to $(0.53\pm0.02)\cdot10^8$ quantum$\cdot$cm^{-2} and in short bioluminescent signal-up to 0.89±0.048 s. Comparison of ctenophore larvae and eggs bioluminescence (Figure 3) detected that larvae light-emission amplitude was eight times and energy-seven times more than eggs had ($P<0.05$).

This tendency was noticed concerning to larvae and eggs signal durations. Larvae signal duration were 2-3 times more than the eggs' one. Ctenophore bioluminescent intensity increased with organism growth. Ctenophore adult individuals bioluminescent intensity exceeded the larvae one. Light-emission duration in the control group 0.63 s more, than in the larvae group.

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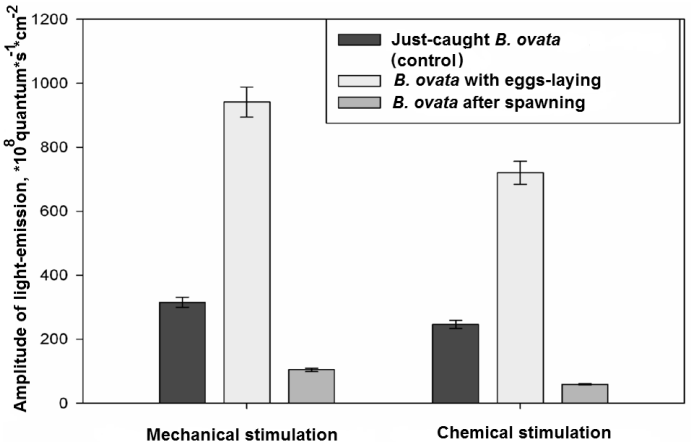

Figure 2. *B. ovata* bioluminescent signal amplitude in reproduction period.

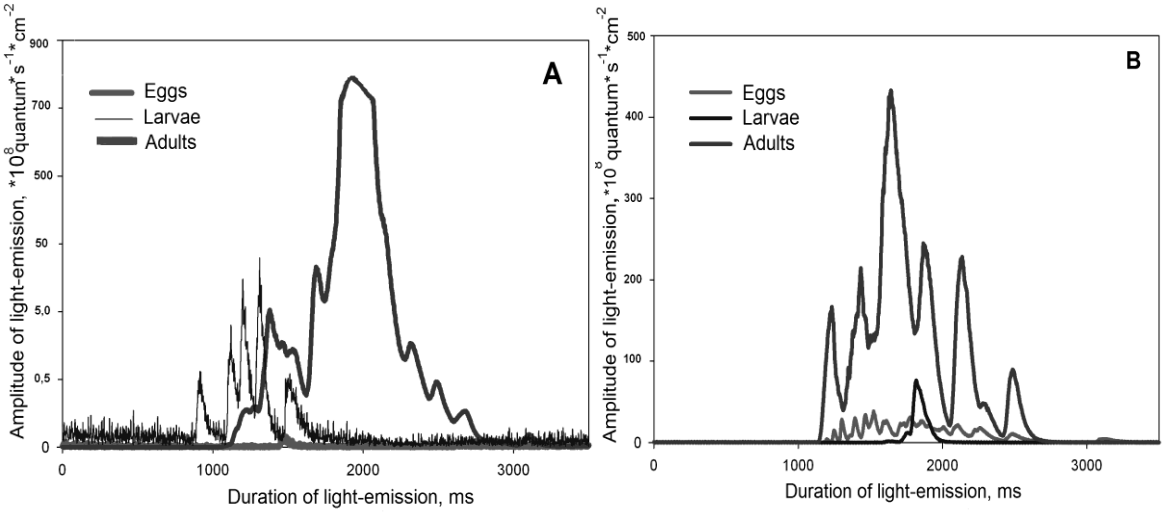

Figure 3. Typical *B. ovata* bioluminescent signals at different ontogeny stages under mechanical (A) and chemical (B) stimulations.

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Thus, the investigations revealed, that bioluminescent characteristics of *B. ovata* change in ontogeny process, at the reproductive stages and increase proportionally with body mass growth.

Discussion

Our investigations were conducted in the period of ctenophore reproduction-from September till November. *B. ovata* spawning peak is observed in October (Arashkevich *et al*., 2001; Finenko *et al*., 2000). Juvenile, eggs and *Beroe* larvae predominated in the zooplankton samples from middle September till October.

As is generally known, that the trophic factor highly affects on ctenophore life activity (Finenko *et al*., 2000) and its bioluminescence characteristics

(Tokarev *et al*., 2008). Thus, according to our data, just-caught ctenophores produced eggs on average in 2-3 day after food digesting. Nevertheless, in case of feeding lack embryo did not achieve larvae stage and died.

The ctenophores in laboratory with enough food supply were similar to the individuals *in situ*, which were located in places of *Mnemiopsis* maximum concentration, so-called "spots" (Finenko *et al*., 2006). In the prespawning period the ctenophores prepare for reproduction, accumulate necessary organic matters and have sufficiently great energetic budget, including eggs energy budget and their own. That is why bioluminescent amplitude-temporal parameters of these ctenophores were maximal in the experiments.

Visual monitoring of *Beroe* behavior in the spawning period revealed, that the individuals after fertilization became less mobile, some of them gravitated to the bottom. The same actions were noticed *in situ*, when ctenophore spawning affected not only their motion behavior but caused death of organisms sometimes (Horoshilov, 1993). The *Beroe* eggs clutch sizes were identical as others authors data (Anninsky *et al*., 2007), when ctenophores in the spawning peak period in the Sevastopol Bay region broadcasted at an average 4500±250 eggs per day. A case is described, when large-sized ctenophore cast out 28,000 eggs, moreover, eggs were broadcasted through a mouth opening (Gucu, 2002). Differences in clutch sizes were caused by different individual sizes, temperature conditions and rate of food supply. The case of ctenophore great numerous eggs broadcasting through the mouth is more likely exception, as *Beroe* cast out eggs through a special tubules-gonoducts in others experiments, including our own. Gonoducts open directly in outdoor environment, not through the mouth.

Mature *B. ovata* individuals as usual lose great quantity of organic matter with reproductive products. Spawning organism with medium length about 53 mm (35–70 mm) loses with reproductive products approximately 14.9% of energy from body mass (Anninsky *et al*., 2005). Ctenophores with body mass 15.4 g loses from 6 to 8% of organic matter per day, from different data, at temperature conditions of 19-21°C (Shiganova *et al*., 2001; Vostokov *et al*., 2001).

In other words, a waste of matter with reproductive products is quite similar to the organism expenses for respiration. This reference to generative strategy of ctenophore metabolism is dominated. Also this explains that the growth come to a halt in reproductive period (Anninsky *et al*., 2007). Accordingly the fact bioluminescence is closely related to biochemical processes in organism and respiration process (Tokarev *et al*., 2008), it is well substantiated that the considerable changes of ctenophore physiological state and metabolism in reproduction period lead to the low bioluminescent parameters of post-spawned individuals, comparing with the control group.

Revealed by our own ctenophore bioluminescent parameters dissimilarity at different reproductive stages, is explained by changes of their biochemical composition in ontogenesis. The eggs and larvae composition of organic matter was much different from the adult individuals (Anninsky *et al*., 2007). Content of organic matter was 4.0±0.8 μg/mg of wet weight in eggs and 67.1±5.7 μg/mg of wet weight in larvae with body length 0.43 mm. The brighter larvae light-emission can be explained by organic great mass content in them.

B. ovata bioluminescent characteristics variability in ontogenesis can be connected with photocyte quantity changes of growing organisms and with their cytological maturity (Shannon, 2002; Shimomura, 2006). Thus, photoprotein and luciferin quantity increase is observed in adult individuals (Shimomura, 2006). It affected at the bioluminescent activity increasing of these organisms. Therefore, the ctenophores bioluminescence quantum output is minimum at early stages of organisms development, and maximum-at late.

To our mind, ctenophore bioluminescent amplitude-temporal variability with body mass increase can be caused also by peculiarities of ctenophore biochemical composition, depending on their sizes.

It is known, that proportion of free amino acid and protein concentration is maximum in small ctenophores (as their metabolism is different by over activity) and minimum in great individuals (Zaika, 2005). Additionally, carbohydrate metabolism apparently influences on ctenophore bioluminescent parameters changes, especially the glycogen contains, which rises in great mature individuals, comparing with juvenile (Anninsky *et al*., 2005).

At the same time, as the organism develops along the way of body growing hydration and active metabolism (Anninsky *et al*., 2007; Zaika, 2005), decrease of great individuals' mobility and manoeuvrability compensate by one of highly-valued quality: the lowered survival capability due to more developed bioluminescent organs and, consequently, maximum bioluminescent energy discharge. We suppose that a protection function of bioluminescence is the most significant component in the ctenophore ecology.

Thus, it is demonstrated that ctenophore bioluminescence is integrated index of its ecology and physiology, which indicates the state of light-emission organisms. That is why a complex research of plankton, including all physiological parameters and bioluminescence among them, is necessary for estimation its functional state.

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