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HOW DIATOM *CYLINDROTHECA CLOSTERIUM* VANQUISH INVASIVE COPEPOD *OITHONA DAVISAE*

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Some diatoms are rich food for herbivorous copepods, while others are toxic for their recruitment. No negative effect of diatom *Cylindrotheca closterium* was ever observed for copepods, and some estuarine copepods preferred it as a food. Data on grazing diatoms by abundant now in the Black Sea coastal waters invasive copepod *Oithona davisae* are still contradictory. Interaction of *O. davisae* and *C. closterium*, both having high colonizing potential and both typical for coastal waters, was studied in experimental culture. Two weeks after inoculation of *C. closterium* the cultured *O. davisae* was drastically fouled by globulous conglomerates of diatom cells. Diatom cells in “colonies” on copepod exoskeleton were interconnected by means of adhesive substances at one of their flexible ends at the point-wise areas at various parts of copepods exoskeleton, and the opposite flexible ends performed various circular roll-over fan-shaped movements around the axis passing through the point of their attachment. “Colonies” behaved as integrated aggressive organisms against any approaching flagellate and prevented normal locomotion of copepods. Herein we present the first report on epizotic behavior of *C. closterium*: quick disastrous colonization of alive copepods *O. davisae* by diatom “colonies” led to total extinction of cyclopoid experimental population while alive diatoms formed dense network on copepods degenerative tissues.

Keywords: diatom, *Cylindrotheca closterium*, colonization, copepod, *Oithona davisae*, Black Sea

Diatoms often dominate in temperate waters during seasonal blooms in winter, early spring and autumn, and had been reputed for a long time as excellent food for herbivorous copepods and the basis for their recruitment. However, in the late 1990s, the copepod-diatom interaction was re-considered when the insidious effect of diatoms on copepod reproduction was found [16]. Diatom-induced inhibition of copepod reproduction was registered in different environments and laboratories proved by field and experimental data. Feeding some species of diatoms can disturb different stages of development of copepods from embryonic to postembryonic related to anti-proliferative action of diatoms associated with low molecular weight aldehydes leading to copepods mortality [8, and literature cited thereafter].

No toxic, or any other negative effect of ubiquitous marine diatom *Cylindrotheca closterium* (Ehrenberg) Reimann & J. C. Lewin, 1964 (Bacillariaceae, Bacillariophycidae) (formerly *Nitzschia closterium*) was observed on reproduction of copepods *Calanus helgolandicus* and *Acartia clausi* [4]. Unlike some other diatom species known to produce toxins, this diatom was never associated with any harmful toxins release, and to date, is widely cultured for far going pharmacological purposes as a transporter of Ag associated nanoparticles [20], or as a source of fucoxanthin [23]. Some coastal harpacticoid copepods even prefer *C. closterium* as a food source to other diatoms [29].

The Black Sea coastal waters were recently invaded by Asian cyclopoid copepod *Oithona davisae*, and nowadays during warm periods it periodically contributes up to 99 % of total copepod abundance in the Sevastopol Bay [2, 25] similar to that observed in its native environment in Tokyo Bay [27]. It is interesting that both diatom *C. closterium* and copepod *O. davisae* have high colonizing potential and are considered typical representatives of the same coastal waters, as for example, Tokyo Bay [18]. *C. closterium* is often found in plankton and is abundant in offshore areas [21]. Study of feeding selectivity of *O. davisae* in natural environment of the Black Sea so far did not reveal feeding on diatoms [13]. Currently, the data on feeding of ambush feeder *O. davisae* on diatoms are contradictory and uncertain [10] while this copepod is often abundant during summer diatom blooms [20]. Herein, the interaction between *O. davisae* and *C. closterium* in experimental culture was studied to find out whether the former can feed on the latter.

MATERIAL AND METHODS

Microalgae culture. Marine semi-benthic tychoplanktonic pennate non-colonial diatom *Cylindrotheca closterium* (Ehrenberg) Reimann & J.C. Lewin, 1964 (Bacillariaceae, Bacillariophycidae) (formerly, synonym *Nitzschia closterium*), cosmopolitan in temperate and tropical waters [11], initially isolated from the Black Sea coastal waters, was kept in the Museum of Alive Phytoplankton Cultures of the Department of Physiology of Algae in A. O. Kovalevsky Institute of Marine Biological Research RAS (former Institute of Biology of the Southern Seas). This species was cultured intensively using new modified artificial medium for mariculture purposes [23], and sub-samples of it from the batch culture were kindly provided for our experiments by Ms Zheleznova S. N.

Copepod culture. Culture of copepod *Oithona davisae* Ferrari and Orsi, 1984, originated from the ovigerous females selected from alive zooplankton samples from the Sevastopol Bay in June 2013, and thereafter was fed cultured cryptophytes IBSS Cr-54 isolate [13]. The sub-culture of copepod was separated in late August 2013, and besides cryptophytes, diatom *C. closterium* was added at initial level 10^3 cells·mL⁻¹, to test this diatom as a possible prey for *O. davisae*, while control culture of *O. davisae* was fed only cryptophytes. The experiment was carried out in two 750 mL (10 cm diameter) glass beakers filled by sterilized by filtration and UV natural Black Sea water 18 salinity. Copepods (only adults and late copepodites, male:female ratio appr. 1:15) were inoculated at initial density appr. 0.1 per mL. Observations were conducted under natural light (var. 3000–7000 lux) and photoperiod appr. 13:11 hrs (light:dark) at (25 ± 2) °C.

Images were obtained using light inverted microscope Nikon Eclipse E200 connected to a video camera: alive copepods – at magnification 4×10 and 10×10 , and various movement modalities of alive microalgae cells – at magnification 10×40 , and processed using free ImageJ software (<http://imagej.nih.gov/ij/>).

RESULTS

Several days after sub-culture of *Cylindrotheca closterium* was added to the sub-culture of *Oithona davisae*, copepods started to decrease their activity. Two weeks after the start of the experiment the copepod movements appeared to be too slow and atypical for this ambush predator. No new nauplii were found in the sub-culture of *O. davisae* where *C. closterium* was added, while control culture of copepods fed only cryptophytes successfully reproduced, and different stages of development including nauplii were observed in it. Thereafter, the copepods from the sub-culture “*O. davisae* – *C. closterium*” were investigated under light inverted microscope to clarify the problem of their “lethargy”.

Microscopic study was carried out 2 weeks after the start of the experiment, and disastrous effect of diatoms on copepods was revealed. All specimens were found fouled but the severity (degree) of infestation varied, possibly, depending on the data of the first attachment of diatom. In less fouled copepods, presumably, at the early stage of infestation, the cells of *C. closterium* attached mainly to the lower part of cephalothorax (Fig. 1A) or to the genital segment (Fig. 1B), forming small ball-shaped conglomerates of cells.

Severely affected by diatoms, most likely infested earlier copepods had the appearance as if their cephalothorax was dressed in a fur coat (Fig. 2A), and their appendages in muffs (Fig. 2B).

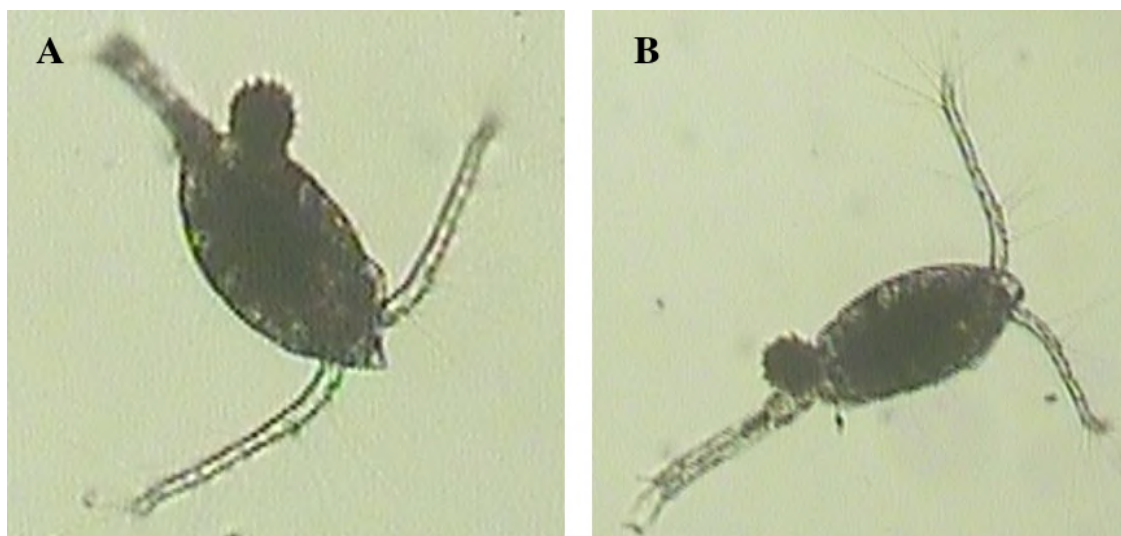


Fig. 1. Start of fouling of *Oithona davisae* carapax by conglomerates of *Cylindrotheca closterium* attached to the lower part of cephalothorax (A) or genital segment near spermatheca (B) of females of *Oithona davisae*. Light inverted microscope Nikon Eclipse E200. Magnification 4×10

Рис. 1. Начало обрастания карапакса *Oithona davisae* конгломератами *Cylindrotheca closterium*, прикреплёнными к нижней части цефалоторакса (A) или к генитальному сегменту около сперматеки (B) самок *Oithona davisae*. Световой микроскоп Nikon Eclipse E200. Увеличение 4×10

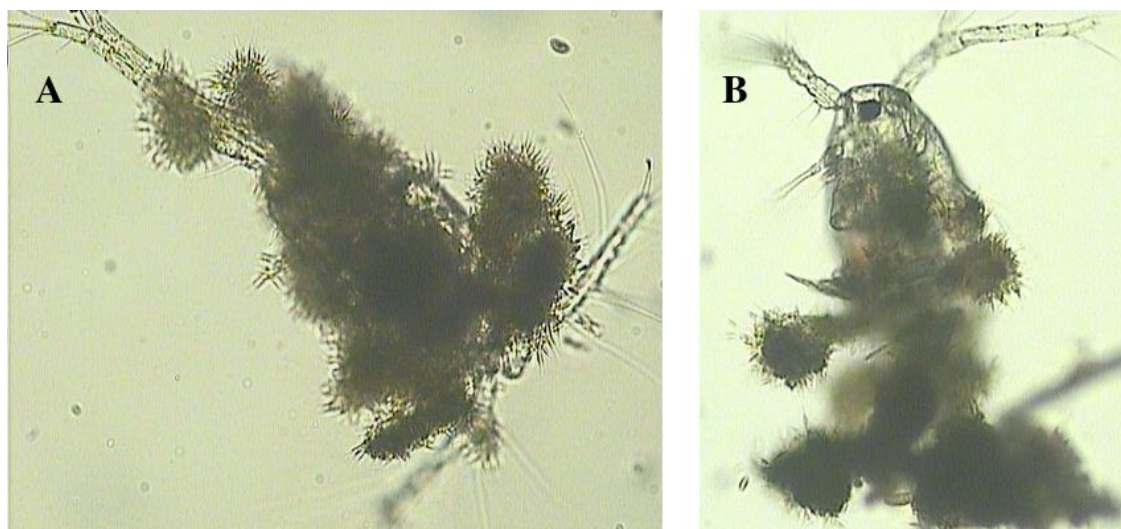


Fig. 2. Late stage of infestation by conglomerates of diatom *Cylindrotheca closterium* on different females of *Oithona davisae*. Light inverted microscope Nikon Eclipse E200. Magnification 10×10

Рис. 2. Поздняя стадия заражения конгломератами диатомовых *Cylindrotheca closterium* разных самок *Oithona davisae*. Световой инвертированный микроскоп Nikon Eclipse E200. Увеличение 10×10

Microscopic investigation and video registration of copepods at higher magnification (40×10) showed that carapaces of *O. davisae* were totally colonized by globulous agglomerates of active movable *C. closterium* cells adhered to different parts of copepods exoskeleton. One of the flexible ends of typical slightly sigmoid lanceolate cells of *C. closterium* were adhered tightly to each other (25–45 cells per cluster) and to a small point-wise area of copepods carapax while the opposite free ends formed small ball-shaped, verticil-like conglomerations of fusiform frustules (Fig. 3). The free flexible ends of *C. closterium* performed composite smooth circular fan-shaped and oscillatory movements around the axis passing through the point of their firm adhesion to substratum (copepod carapax) (video is available as a supplementary file at <https://doi.org/10.21072/mbj.2018.03.3.08>).

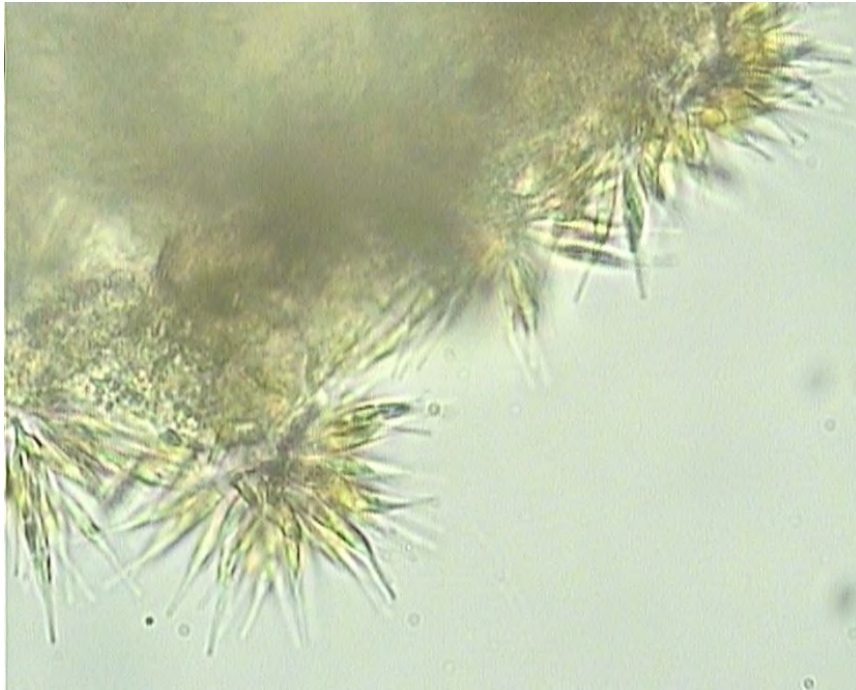


Fig. 3. Urchin-like clusters of movable flexible ends of alive cells of *Cylandrotheca closterium* attached to point-wise areas on carapax of *Oithona davisae*. Light inverted microscope Nikon Eclipse E200. Magnification 10×40

Рис. 3. Ежеподобные пучки подвижных гибких концов живых клеток *Cylandrotheca closterium*, прикреплённых к точечным областям карапакса *Oithona davisae*. Световой инвертированный микроскоп Nikon Eclipse E200. Увеличение 10×40

Three weeks after the start of the experiment we observed on already dead copepod carapax that the cells of *C. closterium* still continued to grow on its degenerative tissues: conglomerates of alive moving diatom cells were found attached elsewhere on carapax of decaying copepod, or attached to the antennula of a dead copepod *O. davisae* (Fig. 4). Free cells of *C. closterium* found nearby substratum area were conducting various movement modalities: “smooth gliding”, “pivot”, and “pirouette” (named so according [3]).

The diatom cells in “colonies” behaved as an integrated aggressive organism injuring approaching cells of alive nanoflagellates. Some of cryptophyte cells were “glued” by mucilageous substances to diatom cells matrix, immobilized (Fig. 4) and died later, while cells of larger microalgae, naked dinoflagellates *Gyrodinium* sp. (when added occasionally) even “glued” to adhesive substances of *C. closterium* were able to detach from adhesive diatom substances (video is available as a supplementary file at <https://doi.org/10.21072/mbj.2018.03.3.08>).

Meanwhile, control culture of *O. davisae* fed cryptophytes reproduced successfully, and in two weeks the second generation of copepods originated from nauplii produced by females (started 2 days after the start of the experiment) reached adulthood.

Our experiment showed that no feeding of copepods, *O. davisae*, on *C. closterium* took place. *Vice versa*, fouled by diatoms *O. davisae* (100 % of copepods) lack mobility and rapidity (obligatory for ambush predator), decreased feeding rate on cryptophytes and ceased reproduction. The impact of diatoms on copepods thereafter logically resulted in complete elimination of copepods experimental population in 5 weeks (more than 90 % of copepods were dead, the remaining were still alive but in poor condition) while diatom population flourished for a long time (minimum a month of observation) on the decomposed copepods remnants. Cells of *C. closterium* formed a dense network on the carapax of the dying and dead *O. davisae* specimens and around it at the bottom of culture vessel (Fig. 5A, 5B), apparently using decomposed organic matter as nutrients.



Fig. 4. Full coverage of antennula of already dead copepod *Oithona davisae* by alive moving cells of *Cylindrotheca closterium*. Free cells of *Cylindrotheca closterium* (below the antennula) are approaching the substrate. Dying oval cryptophyte cell (above antennula) “glued” by EPS (extracellular polymeric substances) to *C. closterium* cells. Light inverted microscope Nikon Eclipse E200. Magnification 10 × 40

Рис. 4. Антеннула погибшей копеподы *Oithona davisae*, полностью покрытая прикрепленными одним концом живыми подвижными клетками *Cylindrotheca closterium*. Свободные клетки *Cylindrotheca closterium* (ниже антеннулы) приближаются к субстрату. Отмирающие овальные клетки криптофитовых водорослей «приклеены» экзополимерными веществами к клеткам *C. closterium*. Световой инвертированный микроскоп Nikon Eclipse E200. Увеличение 10 × 40

DISCUSSION

Many species of pennate diatoms were reported as epibionts on planktonic copepods. Blooming of tychoplanktonic diatom *Cylindrotheca closterium*, common in phytoplankton samples, have been reported in coastal environments, i. e. along the west coast of Southern Baja California in the Gulf of California [9, and references thereafter]. They dominate in planktonic aggregates in Adriatics [1]. Registered as a permanent and abundant species in different Black Sea benthic communities [19, 22] it was listed among the Black Sea phytoplankton species causing blooms with maximum densities attaining 3.2×10^6 cells·L⁻¹ in Varna Bay, 5×10^6 cells·L⁻¹ at Cape Galata [17], (6×10^6) – (13×10^6) cells·L⁻¹ in the Romanian area [5]. The cells of *C. closterium* present permanently in plankton, and can dominate early summer algal blooms (7.4×10^5 cells·L⁻¹ in early July) in the surface waters of the Sinop Bay [28].

Until recently *C. closterium* had not been listed among epizoic species. Discovery of similar epizoic nature and behavior of *C. closterium* on different zooplankton objects in different marine systems, regardless temperature and salinity, was revealed for the first time practically at the same time and independently by several researchers: heavy infestation of *C. closterium* on exoskeleton of a specimen of marine copepod *Paracalanus* sp. found in planktonic sample from the Gulf of California in October 2013 at 28 °C [9]; severe infection of the sea urchin juveniles from St. Lawrence estuary, Canada, at 8 °C in 2016 [15], and fatal colonization of cyclopoid copepod *Oithona davisae* by *C. closterium* revealed in the laboratory experiments in the Black Sea water at 25 °C in September 2013 (reported in this paper). In all three cases similar type of attachment of the cells of *C. closterium* by one of their flexible ends was observed in *Paracalanus* sp. [9], in *O. davisae* (this paper) and in the sea urchin [15].

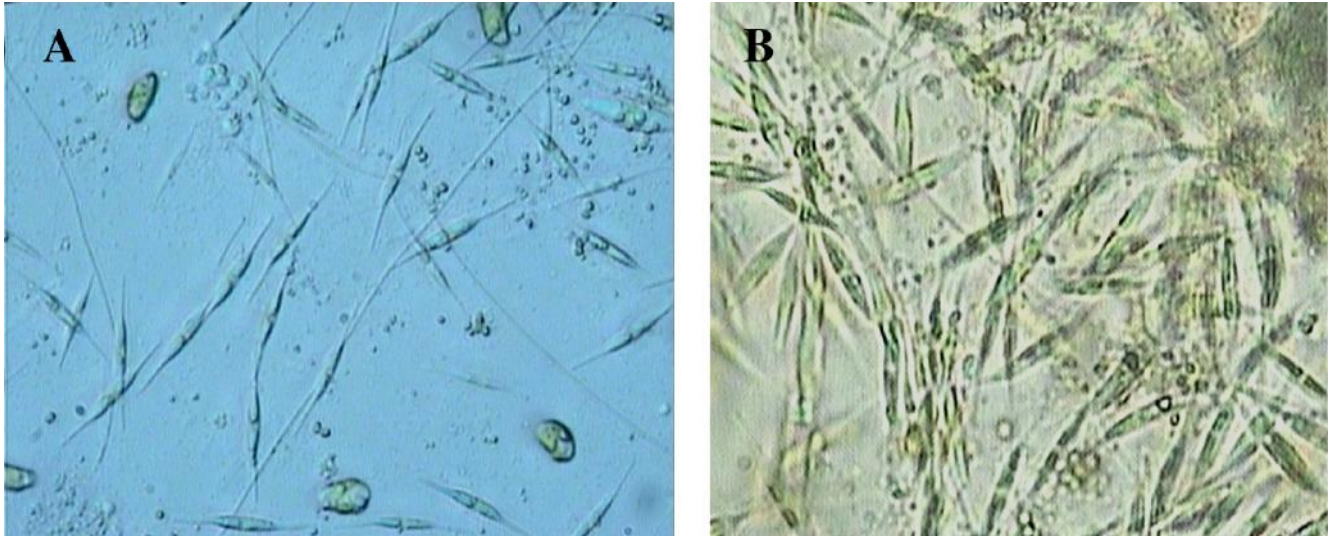


Fig. 5. Cells of *Cylandrotheca closterium* at the bottom of culture vessel. A – ovoid cells of cryptophyte ((16.9 ± 1.4) μm long; (7.1 ± 1.4) μm wide) among lanceolate cells of *C. closterium* (apical axis 30–55 μm ; transapical axis 1.7–3.6 μm). B – alive cells of *C. closterium* forming dense network at the bottom of culture vessel. Light inverted microscope Nikon Eclipse E200. Magnification 10 \times 40

Рис. 5. Клетки *Cylandrotheca closterium*, образующие густую сеть на дне культурального сосуда. А — овалы клетки криптофитовых (($16,9 \pm 1,4$) мкм в длину; ($7,1 \pm 1,4$) мкм в ширину) среди ланцетовидных клеток *C. closterium* (вариации апикальной оси 30–55 мкм; вариации трансапикальной оси 1,7–3,6 мкм). В — живые клетки *C. closterium*, образующие густую сеть на дне культурального сосуда. Световой инвертированный микроскоп Nikon Eclipse E200. Увеличение 10 \times 40

During the process of infestation, the cells of *C. closterium* were linked by exopolymeric substances in clusters of 25–45 per group on the carapax of *O. davisae* (this paper), comparable with appr. 30 per group on the spines of the sea urchin [15] attached to the small areas of substratum. Cells of *C. closterium* colonizing sea urchin juveniles from Canadian waters at 8 °C were distributed in three discrete classes: small cells with length (65 ± 7) μm and width (4.9 ± 0.6) μm ; larger cells with length (112 ± 4) μm and width (5.5 ± 0.6) μm ; and cells without flexible valve ends with length (22 ± 2) μm and width (4.7 ± 0.5) μm [15]. Cells of *C. closterium* proliferating in the culture of *O. davisae* in the Black Sea water at (25 ± 2) °C varied in apical axis from 30 to 55 μm and in transapical axis – from 1.7 to 3.6 μm . The type of cells lacking typical flexible ends, or the cells with flexible ends longer than 15 μm each [15] were never observed in our culture of *C. closterium*, either on the carapaces of copepods, or at the bottom of culture vessels. Differences of the cell morphotypes of *C. closterium* in our work and the work carried out by Magesky et al. [15] could be connected with different conditions of growth of genetically different geographic isolates of diatom.

The main movements of the free ends of the cells of *C. closterium* (attached in clusters by their flexible ends on a point-wise area of *O. davisae* carapax) observed in our study resembled modalities described as “pivot” and “pirouette” with one tip of the cells of *C. closterium* attached to substratum [3] while free cells of *C. closterium* performed mainly “smooth gliding” and “pirouette”. Quick colonization of copepods by diatoms observed in our study is explainable by possibility for active settlement and attachment of cells of *C. closterium* in 30–45 min [21]. More strong and aggregated adhesion of *C. closterium* (*N. closterium*) cells was revealed onto hydrophobic surfaces in contrast to hydrophilic surfaces where diatoms distribute more uniformly [14], hence, chitin of copepods, mainly consisting of highly hydrophobic polysaccharides [6], is likely to be a preferable substrate for diatoms adhesion.

In mechanisms of adherence and locomotion, the expulsion of highly hydrated extracellular polymeric substances (EPS) from the raphe system of diatom is implicated [1, 13]. This process is closely linked to migratory rhythms, light and dark cycles, and the highest levels of EPS are produced under phosphorus limitation. Production of bound EPS closely associated with the diatom

aggregates occurred only in the light and was the highest during the exponential phase [7]. EPS produced by *C. closterium* organizes a web of polysaccharide fibrils with two types of cross-linking: fibrils association forming junction zones and fibril-globule interconnections with globules connecting two or more fibrils; and these flexible fibrils extend up to 15 µm from the cell [26]. Complex mucilaginous matrix of *C. closterium* was considered to be one of the triggers for large aggregates and “marine snow” formation, especially in coastal waters [1]. Our experiments were performed under natural light of high intensity during late summer and early autumn, extra amount of phosphorus initially present in diatom culture medium, was absent in experiment, and these two factors seemed to be enough for the quick expansion of diatoms on copepods exoskeleton. Yet, the infestation behavior of *C. closterium* on the sea urchin juveniles [15] could not be explained by these factors.

According to our results, diatom *C. closterium*, a facultative heterotroph [24], can use hydrophobic surfaces of alive hosts (planktonic copepod *O. davisae*, as example) as substratum; attach to them by self-released EPS rapidly and tightly; form aggressive colonies; stick and immobilize the copepod flagellate prey (presumably due to production of allelopathic chemicals) [12]; damage the host alive tissues; break normal locomotion and behavior of the host decreasing its ability to feed, reproduce and escape from predators; lead to the death of the host, and, thereafter, proliferate on its degenerative tissues in a similar way to that observed for sea urchin [15].

Although results obtained in the laboratory do not always strictly reproduce processes in natural populations, our findings highlight the possibility of tycho planktonic diatom *C. closterium* to affect negatively copepod populations due to biofouling of their exoskeleton, changes in behavioral and, consequently, in their reproduction ecology, possibly, involving copepods into “marine snow” aggregates. The kind of interaction between copepods and diatoms revealed in the present study has identified the need for further research in order to evaluate properly the impact of tycho planktonic diatoms with adhesive properties on copepods population dynamics.

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КАК ДИАТОМОВЫЕ ВОДОРОСЛИ *CYLINDROTHECA CLOSTERIUM* УНИЧТОЖАЮТ ИНВАЗИВНЫХ КОПЕПОД *OITHONA DAVISAE*

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Одни виды диатомовых водорослей являются важным компонентом пищи растительноядных копепод, другие оказываются токсичными для их размножения. До настоящего времени отсутствовали сведения о негативном влиянии диатомовых *Cylindrotheca closterium* на питающихся ими копепод; известно, что некоторые эстуарные копеподы даже предпочитают данный вид другим микроводорослям. Литературные данные по питанию диатомовыми микроводорослями недавних вселенцев в Чёрное море, копепод *Oithona davisae*, противоречивы. В экспериментальной культуре было изучено взаимодействие *O. davisae* и *C. closterium* как двух организмов, обладающих высоким потенциалом колонизации и являющихся типичными для прибрежных вод. Через две недели после инокуляции *C. closterium* в культуру *O. davisae* поверхность тела копепод обрастала шарообразными конгломератами диатомовых клеток. Данные клетки в «колониях» на поверхности тела копепод были связаны между собой и прикреплены с помощью адгезивных веществ одним из гибких концов в точечных областях на разных участках экзоскелета копепод, а противоположные гибкие концы клеток диатомовых выполняли различные круговые веерообразные движения вокруг оси, проходящей через точку их прикрепления. «Колонии» диатомовых вели себя как интегрированные агрессивные организмы против любой приближающейся жгутиковой микроводоросли и препятствовали нормальной локомоции копепод. В данной статье впервые сообщается об эпизоотическом поведении *C. closterium* по отношению к циклопидным копеподам: быстрая катастрофическая колонизация живых *O. davisae* диатомовыми приводит к полной элиминации экспериментальной популяции, в то время как живые клетки диатомовых образуют плотную сетку на дегенеративных тканях отмирающих копепод.

Ключевые слова: диатомовые водоросли, *Cylindrotheca closterium*, обрастание, копеподы, *Oithona davisae*, Чёрное море