

# Sensitivity of dinoflagellates to mechanical stressors as a potential target to control harmful blooms in aquaculture

---

Olga Matantseva, Mariia Berdieva and Ilya Pozdnyakov

*Institute of Cytology, Russian Academy of Sciences, St. Petersburg, 194064, Russia*

| Submitted March 13, 2021 | Accepted April 17, 2021 |

## Summary

Dinoflagellates are diverse and widely spread single-celled eukaryotes causing harmful algal blooms (HABs) in the marine environment. Many dinoflagellate species produce potent toxins that can be accumulated in the tissues of marine organisms, thus posing a threat to the organisms at higher trophic levels, including humans. Harmful dinoflagellate blooms in aquaculture represent a serious problem requiring sustainable solutions. In the first part of this article, we provide a concise review of the existing techniques proposed to control dinoflagellate blooms. In the second part, we discuss sensitivity of dinoflagellates to turbulence/shear stress, as well as a potential approach to control HABs in aquaculture based on this physiological hallmark. We argue that sensitivity of dinoflagellates to turbulence is a prospective target for the effective HAB control and prevention with low ecosystem risks.

**Key words:** aquaculture, dinoflagellates, ecdysis, harmful algal blooms, turbulence, shear stress

## Harmful algal blooms and aquaculture

Outbursts of algal proliferation referred to as harmful algal blooms (HABs) represent one of the major challenges for the aquatic resource management. They deteriorate water quality, affect ecosystem functioning and pose a threat of poisoning to various marine organisms and humans. Dinoflagellates are one of the main groups causing HABs worldwide (Heisler et al., 2008). Several physiological traits make these organisms prone to HAB formation in coastal regions. Many of them are mixotrophs able to obtain nutrients not only in the inorganic forms, but also from dissolved and

particulate organic matter (Burkholder et al., 2008), can tolerate a wide range of salinity and temperature and have resilient stages thought to play an important role in the bloom dynamics (Bravo and Figueroa, 2014).

Although some HABs do not seem to be linked to human activity (Anderson, 2009), the increasing anthropogenic nutrient pollution along with climate change and spread of nonindigenous species to new habitats probably favor further distribution of dinoflagellates and more frequent occurrence of HABs in future (Glibert, 2020). Many data has been acquired over the last decades to understand the reasons and conditions causing HABs and

determining their duration (Anderson, 2009; Glibert and Burford, 2017; Pal et al., 2020; Telesh et al., 2021). Moreover, these data were used to create mathematical models of various complexity aimed at HAB prediction (Glibert et al., 2014; Aleynik et al., 2016; Davidson et al., 2016; Gillibrand et al., 2016; Ralston and Moore, 2020). Nevertheless, the prognostic power of the simpler models can be not sufficient, whereas more elaborate models taking into account complex biological and biogeochemical processes may require significant time and financial investments for their use in practice. Furthermore, model-based predictions can help to avoid some serious consequences of HABs, but do not solve the overall HAB problem.

The most beneficial approach to reduce the number and frequency of blooms is the maintenance of a healthy ecosystem state implying the persistence of a diverse multispecies community and the reduction in pollution of water with anthropogenic nutrients, such as plant fertilizers and sewage (Wells et al., 2019). Unfortunately, in many regions the opposite trend is still observed (Glibert and Burford, 2017; Wurtsbaugh et al., 2019). This is a serious problem, especially for the areas of aquaculture where cultivated marine organisms are destined for human consumption, because, on the one hand, it lifts up risks of human poisoning with dinoflagellate toxins via food supplies, and on the other hand, leads to an economically unfavorable situation when sometimes unjustified precautions limit the mariculture efficiency.

Over the last years, aquaculture-associated dinoflagellate blooms have been registered all over the globe and caused devastating economical losses (Dhaz et al., 2019; Davidson et al., 2021; Kimambo et al., 2021; Trotter et al., 2021). Considering the troubling HABs statistics and expected increase in the aquaculture-sector food production to meet demands of the growing world population (Trotter et al., 2021), elaboration of effective methods involving direct interventions into the ecosystem processes to prevent and combat HABs are highly desirable.

## HAB control technologies

Measures that can be taken to manage HABs include mitigation (actions to reduce negative impacts of HABs, e. g. monitoring and detection of dangerous levels of toxins), prevention (measures to preclude HAB occurrence), and control (actions intended to suppress or destroy ongoing HABs)

(Anderson, 2009). Here we focus on the latter group, but provide only a brief description of the approaches constituting it, necessary as an introduction to the following sections. For a comprehensive information on the existing HAB management strategies, see Anderson (2009), Brown et al. (2019) and references therein.

There are several classes of HAB control methods based on physical, chemical, and biological approaches. Physical methods involve direct removal of HAB organisms, for example, by filtration, sedimentation and burial (Sellner and Rensel, 2018). Sedimentation can be achieved by dispersing clay or modified clay particles that initiate trapping and aggregation (flocculation) of HAB cells. Clay dispersal has been actively used in areas with a significant economic impact of aquaculture, e. g. in South Korea and China (Na et al., 1996; Sengco et al., 2001; Sengco and Anderson, 2004; Yu et al., 2017; Song et al., 2021). Alternatively, HAB cells can be destructed by sonication (Park et al., 2017). However, both removal and lysis approaches are nonspecific and potentially affect not only harmful algae, but also other planktonic organisms. In addition, lysis of HAB cells can lead to the release of dissolved organic matter including toxins, which is another undesired side effect of this method.

Toxic chemicals that can be used to control HABs include natural and synthetic biocidal and biostatic compounds (Gallardo-Rodriguez et al., 2019). Among chemicals suggested to inhibit the activity of marine dinoflagellates and prevent germination of their cysts are copper sulfide (Rounsefell and Evans, 1958), sodium hypochlorite, potassium permanganate (Lam et al., 1995), and hydroxyl radicals (Xiyao et al., 2003). However, they obviously affect not only HAB species, but other ecosystem components too and thus these chemicals have not been applied widely. The examples of more selective and therefore more promising substances to control HABs include free-amine water-soluble chitosan and synthetic peptides tested against *Cochlodinium polykrikoides* (syn. *Margalefidinium polykrikoides*) and *Prorocentrum minimum* (syn. *P. cordatum*) (Park et al., 2016a, 2016b) and N-[(3,4-dichlorophenyl)methyl]cyclohexanamine (DP92) (Cho et al., 2016). At the concentration ranges tested in the lab assays, these compounds were found to be nontoxic to nontarget organisms. Nevertheless, application of chemicals to multispecies mariculture ecosystems still raises environmental concerns.

Biological control methods rely on the activity of viruses, parasites and predators of harmful algae

species. Viruses infecting dinoflagellates are widely spread in nature, they were found to participate in bloom termination and have a high potential to be isolated and used to combat HABs (Tarutani et al., 2001; Nagasaki et al., 2006; Nakayama et al., 2020; Nakayama and Hamaguchi, 2022). Predators able to feed on harmful dinoflagellates and tolerate their toxins can be found among copepods and rotifers (Lacerot et al., 2013), ciliates and dinoflagellates (Jeong et al., 2005; Kamiyama et al., 2005), and parasites are even more diverse and include representatives of bacteria, fungi and protists. Recent years have brought numerous research works on algicidal organisms with bacteria being the main research objects (Zhang et al., 2018, 2020; Shi et al., 2018; Yu et al., 2018). Nevertheless, all biological measures are still risky to use, because they share a common drawback: they can lead to some longterm complications for nonharmful species that are difficult to predict (Gallardo-Rodríguez et al., 2019).

Genetic manipulation aimed at alteration of the physiology of a target organism, e. g. creation of a HAB species unable to produce toxins, is also being investigated. However, concerns associated with it align and in public eyes even exceed those described in the paragraph above, which makes application of the genetic approach a distant goal.

Overall, most HAB control technologies have serious limitations for the use in practice, especially in the open systems. Therefore, alternative approaches are still needed to address the issue of HABs in aquaculture.

### Dinoflagellate sensitivity to mechanical stressors

Dinoflagellates are well known to be extremely sensitive to mechanical stressors of various nature, such as turbulence, mixing, pumping, aeration etc. This peculiar physiological trait hampers the effective culturing of dinoflagellates in laboratory bioreactors (Camacho et al., 2007a; van de Waal et al., 2013; Wang and Lan, 2018). The direct effect of mechanical stressors on microorganisms is attributed to shear forces created by various kinds of agitation. At the spatial scales of microbes, they are described by such flow parameters as the viscous dissipation rate per unit mass  $\varepsilon$  ( $\text{cm}^2\text{s}^{-1}$  or  $\text{ergs g}^{-1}\text{s}^{-1}$ ), the rate of strain  $\gamma = (\varepsilon/\nu)^{1/2}$  ( $\text{rads}^{-1}$ ), and the stress  $\tau = \mu\gamma$  ( $\text{dyne cm}^{-2}$ ), where  $\nu$  is the kinetic viscosity and  $\mu$  is the dynamic viscosity (Thomas and Gibson, 1990a,

1990b). Significant amount of information about the impacts of turbulence on the physiology of dinoflagellates has been published to date, although these parameters have been quantified not in all research works (Table 1).

It was demonstrated *in situ* and under laboratory conditions, that turbulence suppresses growth of dinoflagellates and leads to their mortality when shear stress exceeds certain threshold values. In many cases, suspension in the dinoflagellate growth was linked to the inhibition of the cell division processes (Pollinger and Zemel, 1981; Berdalet, 1992; Wyatt and Jenkinson, 1997; Wong and Kwok, 2005; Llaveria et al., 2009; Martínez et al., 2018; García-Portela et al., 2019). Remarkably, in the study by Pollinger and Zemel (1981) only intermittent turbulence inhibited cell division in *Peridinium cinctum* and only if it was applied in the dark phase of the diurnal cycle. Continuous shaking resulted in high mortality rates for this species.

Furthermore, turbulence caused other physiological responses in dinoflagellates, including the 20% increase in the cellular content of dimethylsulfoniopropionate in *Alexandrium minutum* (Berdalet et al., 2011), termination of phagotrophy in *Peridiniella danica* (Martínez et al., 2018), loss of flagella in *Gonyaulax polyedra* (Thomas and Gibson, 1990a, 1990b), and reduction in the cell size accompanied by other changes in cell morphology in *Ceratocorys horrida* (Zirbel et al., 2000).

In addition, many investigations demonstrated that fluid shear stress induced by agitation or centrifugation triggers ecdysis in dinoflagellates (Bricheux et al., 1992; Haberkorn et al., 2011; Berdieva et al., 2016, 2019, 2020; Matantseva et al., 2020). Ecdysis is a complex process of cell covering rearrangement, which involves shedding of several cell covering elements, including the plasma membrane, outer amphiesmal vesicle membrane and cellulosic thecal plates (if present) with a subsequent re-building of the full amphiesma (Pozdnyakov and Skarlato, 2012). Moreover, it is accompanied by a loss of flagella and thus – by temporal immobility of ecdysing cells (Matantseva et al., 2020). Another pronounced physiological effect associated with turbulence is the induction of bioluminescence in dinoflagellates capable of it (Latz et al., 1994, 1999, 2004; von Dassow et al., 2005; Maldono and Latz, 2007; Heimann et al., 2009; Stires and Latz, 2018; Jalaal et al., 2020).

Fine mechanisms of the initiation and development of the fluid shear stress responses in a dinoflag-

**Table 1.** Dinoflagellate species that respond to turbulence by the growth suspension and/or ecdysis.

Dinoflagellate species	Type of exposure	Reference
<i>Akashiwo sanguinea</i>	natural turbulence generated by wind, upwelling systems	Smayda and Trainer, 2010
	natural turbulence generated by wind, upwelling systems	Smayda, 2010
<i>Alexandrium fundyense</i> (= <i>A. catenella</i> )	turbulence in chamber induced by rods, $\varepsilon = 10^{-4} \text{ m}^2 \text{ s}^{-3}$ ; $10^{-8} \text{ m}^2 \text{ s}^{-3}$	Sullivan and Swift, 2003
<i>Alexandrium minutum</i>	natural turbulence generated by wind	Wyatt and Jenkinson 1997
	continuous turbulence generated by orbital shaker, $\varepsilon^* = 27 \text{ cm}^2 \text{ s}^{-3}$	Llaveria et al., 2009
	continuous turbulence generated by orbital shaker, $\varepsilon^* = 27 \text{ cm}^2 \text{ s}^{-3}$	Berdalet et al., 2011
	centrifugation, 2000 rpm (800 g)	Haberkorn et al., 2011
<i>Amphidinium carterae</i>	Centrifugation, 2000 g	Berdieva et al., 2019
<i>Ceratium</i> sp.	natural turbulence generated by wind, upwelling systems	Smayda, 2010
<i>Ceratium fusus</i> (= <i>Triplos fusus</i> )	turbulence in chamber induced by rods, $\varepsilon = 10^{-4} \text{ m}^2 \text{ s}^{-3}$ ; $10^{-8} \text{ m}^2 \text{ s}^{-3}$	Sullivan and Swift, 2003
<i>Ceratium tripos</i>	turbulence in chamber induced by rods, $\varepsilon = 10^{-4} \text{ m}^2 \text{ s}^{-3}$ ; $10^{-8} \text{ m}^2 \text{ s}^{-3}$	Sullivan and Swift, 2003
<i>Ceratocorys horrida</i>	continuous turbulence generated by orbital shaker, shear stress from $0,012 \pm 0,028 \times 10^{-3} \text{ N}\cdot\text{m}^{-2}$ to $3,196 \pm 1,413 \times 10^{-3} \text{ N}\cdot\text{m}^{-2}$	Zirbel et al., 2000
	natural turbulence generated by wind, upwelling systems	Smayda, 2010
<i>Cryptocodinium cohnii</i>	continuous orbital shaking, 150 rpm or 200 rpm (shear stress= from 0,002 to 0,004 $\text{N m}^{-2}$ )	Yeung and Wong, 2003
<i>Dinophysis acuminata</i>	turbulence induced by oscillating grids, $\varepsilon = 0,5\text{-}8 \times 10^{-6} \text{ m}^2 \text{ s}^{-3}$ ; $0,3\text{-}4 \times 10^{-5} \text{ m}^2 \text{ s}^{-3}$ ; $0,5\text{-}4 \times 10^{-4} \text{ m}^2 \text{ s}^{-3}$	García-Portela et al., 2019
<i>Dinophysis acuta</i>	turbulence induced by oscillating grids, $\varepsilon = 0,5\text{-}8 \times 10^{-6} \text{ m}^2 \text{ s}^{-3}$ ; $0,3\text{-}4 \times 10^{-5} \text{ m}^2 \text{ s}^{-3}$ ; $0,5\text{-}4 \times 10^{-4} \text{ m}^2 \text{ s}^{-3}$	García-Portela et al., 2019
<i>Glenodinium foliaceum</i> (= <i>Kryptoperidinium foliaceum</i> )	centrifugation, 810 rpm	Bricheux et al., 1992
<i>Gymnodinium catenatum</i>	turbulence in chamber induced by rods, $\varepsilon = 10^{-4} \text{ m}^2 \text{ s}^{-3}$ ; $10^{-8} \text{ m}^2 \text{ s}^{-3}$	Sullivan and Swift, 2003
<i>Gymnodinium nelsonii</i> (= <i>Akashiwo sanguinea</i> )	turbulence induced by circular polyethylene grid oscillating up and down, 20 rpm	Berdalet, 1992
<i>Gyrodinium dominans</i>	turbulence induced by oscillating inox grids, $\varepsilon = 1,2 \times 10^{-2} \text{ cm}^2 \text{ s}^{-3}$	Martínez et al., 2018
<i>Heteroscapsa triquetra</i> (= <i>Kryptoperidinium triquetrum</i> )	continuous orbital shaking, 150 rpm or 200 rpm (shear stress= from 0,002 to 0,004 $\text{N m}^{-2}$ )	Yeung and Wong, 2003
<i>Karlodinium veneficum</i>	flow in chamber, fluid density= $1030 \text{ kg m}^{-3}$ fluid viscosity= $1,3 \times 10^{-3} \text{ Pa s}$	Gallardo-Rodríguez et al., 2016
<i>Lingulodinium polyedra</i> (= <i>Gonyaulax polyedra</i> )	Couette flow, cylinder rotation= 8 rpm ( $17 \text{ rad s}^{-1}$ ); 20 rpm ( $44 \text{ rad s}^{-1}$ )	Gibson and Thomas, 1995
	Couette flow, shear stress= from 0,3 to 16,6 $\text{dyn cm}^{-2}$	Latz et al., 1994
	flow in chamber, flow rates/shear stress= 1 $\text{ml min}^{-1}$ / 0,63 Pa; 2 $\text{ml min}^{-1}$ / 1,25 Pa; 3 $\text{ml min}^{-1}$ / 1,88 Pa; 4 $\text{ml min}^{-1}$ / 2,5 Pa	Mallipattu et al., 2002
	turbulence in chamber induced by rods, $\varepsilon = 10^{-4} \text{ m}^2 \text{ s}^{-3}$ ; $10^{-8} \text{ m}^2 \text{ s}^{-3}$	Sullivan and Swift, 2003
	stirring by rod, 2000 rpm	Stires and Latz, 2018
<i>Oxyrrhis marina</i>	turbulence induced by oscillating inox grids, $\varepsilon = 1,2 \times 10^{-2} \text{ cm}^2 \text{ s}^{-3}$	Martínez et al., 2018
<i>Peridiniella danica</i>	turbulence induced by oscillating inox grids, $\varepsilon = 1,2 \times 10^{-2} \text{ cm}^2 \text{ s}^{-3}$	Martínez et al., 2018
<i>Peridinium cinctum</i> forma <i>westii</i>	continuous rotary shaking or intermittent shaking, 100 $\text{r min}^{-1}$	Pollinger and Zemel, 1981

**Table 1.** Continuation.

<i>Prorocentrum cordatum</i>	Centrifugation, $\geq 500$ g	Matantseva et al., 2020
<i>Protoceratium reticulatum</i>	flow in chamber, fluid density= $1030 \text{ kg m}^{-3}$ fluid viscosity= $1,3 \times 10^{-3} \text{ Pa s}$	Gallardo-Rodríguez et al., 2016
<i>Pyrocystis fusiformis</i>	Couette flow, shear stress= from 0,3 to 16,6 $\text{dyn cm}^{-2}$	Latz et al., 1994
<i>Pyrocystis lunula</i>	stirring on a magnetic stirrer	Heimann et al., 2009
<i>P. noctiluca</i> (= <i>P. pseudonocluca</i> )	Couette flow, shear stress= from 0,3 to 16,6 $\text{dyn cm}^{-2}$	Latz et al., 1994
	turbulence in chamber induced by rods, $\epsilon = 10^{-4} \text{ m}^2 \text{ s}^{-3}$ ; $10^{-8} \text{ m}^2 \text{ s}^{-3}$	Sullivan and Swift, 2003
<i>S. hexapraecingula</i>	high-pressure treatment in piston-cylinder-type pressure chamber, 69–196 MPa	Sekida et al., 2012

ellate cell are still to be elucidated, but some data have already been obtained. It was shown that shear stress increased the plasma membrane fluidity in *Lingulodinium polyedrum* (syn. *Gonyaulax polyedra*) (Mallipattu et al., 2002) and *Protoceratium reticulatum* (Gallardo-Rodríguez et al., 2012, 2016). Abrupt changes in the membrane fluidity can be sensed by mechanoreceptors and further transduced to the respective cellular targets by means of one or another signaling pathway, as it was shown to occur in animal cells (Ingber, 2006; White and Frangos, 2007).

### Dinoflagellate sensitivity to turbulence as a potential target to control their blooms

Until now, there is no widely accepted and applied method to prevent and control HABs. Clay dispersal, which is considered the most promising currently used technique, is not selective and affects different planktonic organisms; moreover, each flocculant requires thorough investigations to test it for toxicity and accumulation in tissues of marine organisms (Gallardo-Rodríguez et al., 2019). We assume that sensitivity of dinoflagellates to turbulence can be used as a target to combat their blooms. Natural turbulence generated by wind and wave activity or in the regions of upwelling can trigger ecdysis and inhibit growth of dinoflagellates in the sea (Wyatt and Jenkinson, 1997; Smayda, 2010; Smayda and Trainer, 2010). It is recognized as one of the significant factors influencing the bloom dynamics with increased turbulence resulting in fast bloom termination (Shutler et al., 2015) and reduced turbulence associated with the initiation of HABs (Brown et al., 2020).

Turbulence generated artificially by means of pumping or another engineering approach could become an environmentally friendly and effective

solution for the HAB problem at aquaculture sites. This approach would be selective to dinoflagellates, since they are the most turbulence-sensitive marine protists (Thomas and Gibson, 1990a; Wang and Lan, 2018; Arnott et al., 2021) and therefore, even low levels of artificially-induced turbulence comparable to those found in natural ecosystems have a potential to suspend their growth with no negative effect on other groups of organisms. Generation of turbulence at large scales may seem difficult to achieve, but water- and air-pumping systems have been applied to aquaculture before to mix the water column and thus impair algae buoyancy or remove them from a photic zone (Brown et al., 2020). Moreover, airlift upwelling is used in salmon farms to bring deep water free of algae to the cages (Gallardo-Rodríguez et al., 2019).

Pumping systems operating at large scales require a lot of energy, but solar power solutions are already available (Vo et al., 2021). Moreover, laboratory studies demonstrate that intermittent turbulence would be sufficient to suppress the dinoflagellate growth (Pollinger and Zemel, 1981; Gibson and Thomas, 1995). If intermittent turbulence is applied in the dark time of a day, as it was the case in the work by Pollinger and Zemel (1981), diurnal vertical migration typical to dinoflagellates (Cullen, 1985; Olsson and Granéli, 1991) has to be taken into account to choose the optimal depth for water agitation.

One of the advantages of the suggested approach would be an ability to regulate the intensity of turbulence/shear stress depending on the aims. With the support of the model-based HAB forecasts, generation of artificial turbulence of lower intensity could prevent initiation of a blooming event, whereas turbulence of high intensity could be applied to disrupt an ongoing dinoflagellate bloom. A possibility to suspend growth of dinoflagellates

and not to destruct their cells at the same time is also beneficial, since such action would not be associated with nutrients and toxins release from cells.

Potential shortcomings of the turbulence-based HAB control approach may be linked to still incomplete understanding of the extremely complex, direct and indirect, phytoplankton-turbulence interactions that are reviewed by Arnott with co-authors (Arnott et al., 2021). Some unexpected negative ecosystem consequences of the artificial water agitation cannot be excluded, although their probability does not seem high, given the low turbulence intensity sufficient to affect dinoflagellates, its plausible intermittent use and possible horizontal application that would not involve vertical mixing disrupting the water column gradients.

In order to translate the idea of using dinoflagellate sensitivity to turbulence/shear stress into practice, more research on different bloom-forming dinoflagellate species is needed. Additionally, the transfer of the existing approaches to generate artificial turbulence from the lab and mesocosm studies (see Arnott et al., 2021 for a review of such methods and key phytoplankton-turbulence laboratory experiments) to larger aquaculture systems is required. Such studies should involve a tight collaboration of ecologists with the experts in fluid dynamics and engineers.

## Acknowledgements

This work was supported by the Russian Science Foundation, project No 18-74-10093.

## References

- Aleynik D., Dale A.C., Porter M. and Davidson K. 2016. A high resolution hydrodynamic model system suitable for novel harmful algal bloom modelling in areas of complex coastline and topography. *Harmful Algae*. 53, 102–117.
- Anderson D. 2009. Approaches to monitoring, control and management of harmful algal blooms (HABs). *Ocean Coast. Manag.* 52, 342–347.
- Arnott R.N., Cherif M., Bryant L.D. and Wain D.J. 2021. Artificially generated turbulence: a review of phycological nanocosm, microcosm, and mesocosm experiments. *Hydrobiologia*. 848, 1–31.
- Berdalet E. 1992. Effects of turbulence on the marine dinoflagellate *Gymnodinium nelsonii*. *J. Phycol.* 28, 267–272.
- Berdalet E., Llaveria G. and Simy R. 2011. Modulation of dimethylsulfoniopropionate (DM SP) concentration in an *Alexandrium minutum* (Dinophyceae) culture by small-scale turbulence: A link to toxin production? *Harmful Algae*. 11, 88–95.
- Berdieva M., Pechkovskaya S. and Matantseva O. 2020. Tetracycline and the ecdysis level in cultures of the dinoflagellate *Prorocentrum minimum*. *Protistology*. 14, 246–251.
- Berdieva M., Safonov P. and Matantseva O. 2019. Ultrastructural aspects of ecdysis in the dinoflagellate *Amphidinium carterae*. *Protistology*. 13, 57–63.
- Berdieva M., Skarlato S., Matantseva O. and Pozdnyakov I. 2016. Mechanical impact on the cell covering fine structure of dinoflagellates *Prorocentrum cordatum*. *Tsitologiya*. 58, 792–798.
- Bravo I. and Figueroa R.I. 2014. Towards an ecological understanding of dinoflagellate cyst functions. *Microorganisms*. 2, 11–32.
- Bricheux G., Mahoney D.G. and Gibbs S.P. 1992. Development of the pellicle and thecal plates following ecdysis in the dinoflagellate *Glenodinium foliaceum*. *Protoplasma*. 168, 159–171.
- Brown A.R., Lilley M., Shutler J., Lowe C., Artioli Y., Torres R., Berdalet E. and Tyler C.R. 2020. Assessing risks and mitigating impacts of harmful algal blooms on mariculture and marine fisheries. *Rev. Aquacult.* 12, 1663–1688.
- Burkholder J.M., Glibert P.M. and Skelton H.M. 2008. Mixotrophy, a major mode of nutrition for harmful algal species in eutrophic waters. *Harmful Algae*. 8, 77–93.
- Camacho F.G., Rodríguez J.G., Miryn A.S., Garcha M.C., Belarbi E.H., Chisti Y. and Grima E.M. 2007a. Biotechnological significance of toxic marine dinoflagellates. *Biotechnol. Adv.* 25, 176–194.
- Camacho F.G., Rodríguez J.G., Miryn A.S., Garcha M.C., Belarbi E.H. and Grima E.M. 2007b. Determination of shear stress thresholds in toxic dinoflagellates cultured in shaken flasks: implications in bioprocess engineering. *Process Biochem.* 42, 1506–1515.
- Cho Y., Cho K.H., Cho H. and Jee J.P. 2016. Development of cationic liposomes for enhanced algicidal efficacy of the novel algicidal agent DP92. *Bull. Korean Chem. Society*. 37, 1086–1094.
- Cullen J.J. 1985. Diel vertical migration by dinoflagellates: roles of carbohydrate metabolism and behavioral flexibility. *Contrib. Mar. Sci.* 27, 135–152.
- Davidson K., Anderson D.M., Mateus M., Reguera B., Silke J., Sourisseau M. and Maguire J.

2016. Forecasting the risk of harmful algal blooms. *Harmful Algae*. 53, 1–7.

Davidson K., Whyte C., Aleynik D., Dale A., Gontarek S., Kurekin A.A., McNeill S. et al. 2021. HAB reports: online early warning of harmful algal and biotoxin risk for the Scottish shellfish and finfish aquaculture industries. *Front. Mar. Sci.* 8, 350.

Díaz P.A., Álvarez G., Varela D., Pérez-Santos I., Díaz M., Molinet C., Seguel M. et al. 2019. Impacts of harmful algal blooms on the aquaculture industry: Chile as a case study. *Perspect. Phycol.* 6, 39–50.

Donaghay P.L. and Osborn T.R. 1997. Toward a theory of biological-physical control of harmful algal bloom dynamics and impacts. *Limnol. Oceanogr.* 42, 1283–1296.

Gallardo-Rodríguez J.J., Astuya-Villalon A., Llanos-Rivera A., Avello-Fontalba V. and Ulloa-Jofre V. 2019. A critical review on control methods for harmful algal blooms. *Rev. Aquacult.* 2019, 661–684.

Gallardo-Rodríguez J.J., García-Camacho F., Sánchez-Mirón A., López-Rosales L., Chisti Y. and Molina-Grima E. 2012. Shear-induced changes in membrane fluidity during culture of a fragile dinoflagellate microalga. *Biotechnol. Progr.* 28, 467–473.

Gallardo-Rodríguez J.J., López-Rosales L., Sánchez-Mirón A., García-Camacho F., Molina-Grima E. and Chalmers J.J. 2016. New insights into shear-sensitivity in dinoflagellate microalgae. *Bioresource Technol.* 200, 699–705.

García-Portela M., Reguera B., d'Alcala M.R., Rodríguez F. and Montresor M. 2019. Effects of small-scale turbulence on two species of *Dinophysis*. *Harmful Algae*. 89, 101654.

Gibson C.H. and Thomas W.H. 1995. Effects of turbulence intermittency on growth inhibition of a red tide dinoflagellate, *Gonyaulax polyedra* Stein. *J. Geophys. Res.: Oceans*. 100, 24841–24846.

Gillibrand P.A., Siemering B., Miller P.I. and Davidson K. 2016. Individual-based modelling of the development and transport of a *Karenia miki-motoi* bloom on the North-west European continental shelf. *Harmful Algae*. 53, 118–134.

Glibert P.M. 2020. Harmful algae at the complex nexus of eutrophication and climate change. *Harmful Algae*. 91, 101583.

Glibert P.M., Allen I.J., Artioli Y., Beusen A., Bouwman L., Harle J., Holmes R. and Holt J. 2014. Vulnerability of coastal ecosystems to changes in harmful algal bloom distribution in response to

climate change: projections based on model analysis. *Glob. Change Biol.* 20, 3845–3858.

Glibert P.M. and Burford M.A. 2017. Globally changing nutrient loads and harmful algal blooms: recent advances, new paradigms, and continuing challenges. *Oceanography*. 30, 58–69.

Haberkorn H., Hégaret H., Marie D., Lambert C. and Soudant P. 2011. Flow cytometric measurements of cellular responses in a toxic dinoflagellate, *Alexandrium minutum*, upon exposure to thermal, chemical and mechanical stresses. *Harmful Algae*. 10, 463–471.

Heimann K., Klerks P.L. and Hasenstein K.H. 2009. Involvement of actin and microtubules in regulation of bioluminescence and translocation of chloroplasts in the dinoflagellate *Pyrocystis lunula*. *Bot. Mar.* 52, 170–77.

Heisler J., Glibert P.M., Burkholder J.M., Anderson D.M., Cochlan W., Dennison W.C., Dortch Q. et al. 2008. Eutrophication and harmful algal blooms: a scientific consensus. *Harmful Algae*. 8, 3–13.

Ingber D. E. 2006. Cellular mechanotransduction: putting all the pieces together again. *FASEB J.* 20, 811–827.

Jalaal M., Schramma N., Dode A., De Malep-rade H., Raufaste C. and Goldstein R.E. 2020. Stress-induced dinoflagellate bioluminescence at the single cell level. *Phys. Rev. Lett.* 125, 028102.

Jeong H.J., Jae S.K., Jong H.K., Seong T.K., Kyeong A.S., Tae H.K., Song J.E. et al. 2005. Feeding and grazing impact of the newly described heterotrophic dinoflagellate *Stoeckeria algicida* on the harmful alga *Heterosigma akashiwo*. *Mar. Ecol. Prog. Ser.* 295, 69–78.

Juhl A.R. and Latz M.I. 2002. Mechanisms of fluid shear-induced inhibition of population growth in a red-tide dinoflagellate. *J. Phycol.* 38, 683–694.

Kamiyama T., Tsujino M., Matsuyama Y. and Uchida T. 2005. Growth and grazing rates of the tintinnid ciliate *Favella taraikaensis* on the toxic dinoflagellate *Alexandrium tamarense*. *Mar. Biol.* 147, 989–997.

Kimambo O.N., Gumbo J.R., Chikoore H. and Msagati T.A.M. 2021. Harmful algal blooms in aquaculture systems in Ngerengere Catchment, Morogoro, Tanzania: stakeholder's experiences and perception. *Int. J. Environ. Res. Public Health* 18, 4928.

Lacerot G., Kruk C., Lüring M. and Scheffer M. 2013. The role of subtropical zooplankton as grazers of phytoplankton under different predation

levels. *Freshwat. Biol.* 58, 494–503.

Lam A.K.-Y., Prepas E.E., Spink D. and Hruddy S.E. 1995. Chemical control of hepatotoxic phytoplankton blooms: implications for human health. *Water Res.* 29, 1845–1854.

Latz M.I., Case J.F. and Gran R.L. 1994. Excitation of bioluminescence by laminar fluid shear associated with simple Couette flow. *Limnol. Oceanogr.* 39, 1424–1439.

Latz M.I., Nauen J.C. and Rohr J. 2004. Bioluminescence response of four species of dinoflagellates to fully developed pipe flow. *J. Plankton Res.* 26, 1529–1546.

Latz M.I. and Rohr J. 1999. Luminescent response of the red tide dinoflagellate *Lingulodinium polyedrum* to laminar and turbulent flow. *Limnol. Oceanogr.* 44, 1423–1435.

Llaveria G., Figueroa R.I., Garces E. and Berdalet E. 2009. Cell cycle and cell mortality of *Alexandrium minutum* (Dinophyceae) under small-scale turbulence conditions. *J. Phycol.* 45, 1106–1115.

Maldonado E.M. and Latz M.I. 2007. Shear-stress dependence of dinoflagellate bioluminescence. *Biol. Bull.* 212, 242–249.

Mallipattu S.K., Haidekker M., Von Dassow P., Latz M. and Frangos J. 2002. Evidence for shear-induced increase in membrane fluidity in the dinoflagellate *Lingulodinium polyedrum*. *J. Comp. Physiol. A.* 188, 409–416.

Martínez R.A., Calbet A. and Saiz E. 2018. Effects of small-scale turbulence on growth and grazing of marine microzooplankton. *Aquat. Sci.* 80, 2.

Matantseva O., Berdieva M., Kalinina V., Pozdnyakov I., Pechkovskaya S. and Skarlato S. 2020. Stressor-induced ecdysis and thecate cyst formation in the armoured dinoflagellates *Prorocentrum cordatum*. *Sci. Rep.* 10, 18322.

Nagasaki K., Tomaru Y., Shirai Y., Takao Y. and Mizumoto H. 2006. Dinoflagellate-infecting viruses. *J. Mar. Biol. Assoc. UK.* 86, 469–474.

Nakayama N. and Hamaguchi M. 2022. The importance of the genetic diversity of the HcRNAV ssRNA virus in the viral-based bloom control of the dinoflagellate *Heterocapsa circularisquama*. *Aquaculture.* 546, 737318.

Nakayama N., Hamaguchi M., Yamaguchi H., Masuda K. and Fujiwara M. 2020. Evaluation of a virus-based control method to protect cultured oysters from the harmful dinoflagellate *Heterocapsa circularisquama*. *Aquaculture.* 529, 735625.

Olsson P. and Granéli E. 1991. Observations on diurnal vertical migration and phased cell division

for three coexisting marine dinoflagellates. *J. Plankton Res.* 13, 1313–1324.

Pal M., Yesankar P.J., Dwivedi A. and Qureshi A. 2020. Biotic control of harmful algal blooms (HABs): A brief review. *J. Environ. Manag.* 268, 110687.

Park S.-C., Choi C., Jeong G.-W., Lee H.-S., Choi S.-J., Kim W.-S. and Nah J.-W. 2016a. Algicidal effects of free-amine water-soluble chitosan to marine harmful algal species. *J. Ind. Eng. Chem.* 34, 139–145.

Park S.-C., Moon J.C., Kim N.-H., Kim E.-J., Jeong J.-E., Nelson A.D.L., Jo B.-H. et al. 2016b. Algicidal effect of hybrid peptides as potential inhibitors of harmful algal blooms. *Biotechnol. Lett.* 38, 847–854.

Park J., Church J., Son Y., Kim K.T. and Lee W.H. 2017. Recent advances in ultrasonic treatment: challenges and field applications for controlling harmful algal blooms (HABs). *Ultrason. Sonochem.* 38, 326–334.

Pollinger U. and Zemel E. 1981. In situ and experimental evidence of the influence of turbulence on cell division processes of *Peridinium cinctum* forma *westii* (leemm.) Lefèvre. *Br. Phycol. J.* 16, 281–287.

Pozdnyakov I. and Skarlato S. 2012. Dinoflagellate amphiesma at different stages of the life cycle. *Protistology.* 7, 108–115.

Ralston D.K. and Moore S.K. 2020. Modeling harmful algal blooms in a changing climate. *Harmful Algae.* 91, 101729.

Rounsefell G.A. and Evans J.E. 1958. Large-scale experimental test of copper sulfate as a control for the Florida red tide. US Fish Wildlife Service, special science report 270.

Sellner K.G. and Rensel J.E. 2018. Prevention, control and mitigation of Harmful Algal Bloom impacts on fish shellfish and human consumers. In: *Harmful Algal Blooms a Compendium Desk Reference* (Eds: Shumway S.E., Burkholder J.M., Morton S.L.). John Wiley & Sons Inc., Hoboken, NJ, pp. 435–492.

Sengco M.R. and Anderson D.M. 2004. Controlling harmful algal blooms through clay flocculation 1. *J. Eukaryot. Microbiol.* 51, 169–172.

Sengco M.R., Li A., Tugend K., Kulis D. and Anderson D.M. 2001. Removal of red-and brown-tide cells using clay flocculation. I. Laboratory culture experiments with *Gymnodinium breve* and *Aureococcus anophagefferens*. *Mar. Ecol. Prog. Ser.* 210, 41–53.

Shi X., Liu L., Li Y., Xiao Y., Ding G., Lin



- S. and Chen J. 2018. Isolation of an algicidal bacterium and its effects against the harmful-algal-bloom dinoflagellate *Prorocentrum donghaiense* (Dinophyceae). *Harmful Algae*. 80, 72–79.
- Smayda T.J. 2010. Adaptations and selection of harmful and other dinoflagellate species in upwelling systems. 2. Motility and migratory behaviour. *Prog. Oceanogr.* 85, 71–91.
- Smayda T.J. and Trainer V.L. 2010. Dinoflagellate blooms in upwelling systems: Seeding, variability, and contrasts with diatom bloom behaviour. *Prog. Oceanogr.* 85, 92–107.
- Song X., Zhang Y. and Yu Z. 2021. An eco-environmental assessment of harmful algal bloom mitigation using modified clay. *Harmful Algae*. 107, 102067.
- Sullivan J.M. and Swift E. 2003. Effects of small-scale turbulence on net growth rate and size of ten species of marine dinoflagellates. *J. Phycol.* 39, 83–94.
- Shutler J.D., Warren M.A., Miller P.I., Barciela R., Mahdon R., Land P.E., Edwards K. et al. 2015. Operational monitoring and forecasting of bathing water quality through exploiting satellite Earth observation and models: the AlgaRisk demonstration service. *Comput. Geosci.* 77, 87–96.
- Stires J. C. and Latz M. I. 2018. Contribution of the cytoskeleton to mechanosensitivity reported by dinoflagellate bioluminescence. *Cytoskeleton*. 75, 12–21.
- Tarutani K., Nagasaki K., Itakura S. and Yamaguchi M. 2001. Isolation of a virus infecting the novel shellfish-killing dinoflagellate *Heterocapsa circularisquama*. *Aquat. Microb. Ecol.* 23, 103–111.
- Telesh I., Schubert H. and Skarlato S. 2021. Abiotic stability promotes dinoflagellate blooms in marine coastal ecosystems. *Estuar. Coast. Shelf Sci.* 251, 107239.
- Thomas W.H. and Gibson C.H. 1990a. Effects of small-scale turbulence on microalgae. *J. Appl. Phycol.* 2, 71–77.
- Thomas W.H. and Gibson C.H. 1990b. Quantified small-scale turbulence inhibits a red tide dinoflagellate, *Gonyaulax polyedra* Stein. *Deep Sea Res. Part A*. 37, 1583–1593.
- Trottet A., George C., Drillet G. and Lauro F.M. 2021. Aquaculture in coastal urbanized areas: a comparative review of the challenges posed by harmful algal blooms. *Crit. Rev. Environ. Sci. Tech.* Ahead-of-print, 1–42. doi:10.1080/10643389.2021.1897372.
- van de Waal D.B., Eberlein T., Bublitz Y., John U. and Rost B. 2014. Shake it easy: a gently mixed continuous culture system for dinoflagellates. *J. Plankton Res.* 36, 889–894.
- Vo T.T.E., Ko H., Huh J.H., and Park N. 2021. Overview of solar energy for aquaculture: the potential and future trends. *Energies*. 14, 6923.
- von Dassow P., Bearon R.N. and Latz M.I. 2005. Bioluminescent response of the dinoflagellate *Lingulodinium polyedrum* to developing flow: Tuning of sensitivity and the role of desensitization in controlling a defensive behavior of a planktonic cell. *Limnol. Oceanogr.* 50, 607–619.
- Wang C. and Lan C.Q. 2018. Effects of shear stress on microalgae – a review. *Biotechnol. Adv.* 36, 986–1002.
- Wang Y., Li S., Liu G., Li X., Yang Q., Xu Y., Hu Z. et al. 2020. Continuous production of algicidal compounds against *Akashiwo sanguinea* via a *Vibrio* sp. co-culture. *Bioresour. Technol.* 295, 122246.
- Wells M.L., Karlson B., Wulff A., Kudela R., Trick C., Asnaghi V., Berdalet E. et al. 2020. Future HAB science: directions and challenges in a changing climate. *Harmful Algae*. 91, 101632.
- White C.R. and Frangos J.A. 2007. The shear stress of it all: the cell membrane and mechanochemical transduction. *Philos. Trans. R. Soc. B*. 362, 1459–1467.
- Wong J.T. and Kwok A.C. 2005. Proliferation of dinoflagellates: blooming or bleaching. *Bioessays*. 27, 730–740.
- Wurtsbaugh W.A., Paerl H.W. and Dodds W.K. 2019. Nutrients, eutrophication and harmful algal blooms along the freshwater to marine continuum. *Wiley Interdiscip. Rev.: Water*. 6, e1373.
- Wyatt T. and Jenkinson I.R. 1997. Notes on *Alexandrium* population dynamics. *J. Plankton Res.* 19, 551–575.
- Xiyao B., Zhou X., Lu J., Zong X. and Huang G. 2003. Experiment of killing the microorganisms of red tide using hydroxyl radicals in the shore of Jiaozhou gulf. *J. Dalian Maritime University*. 29, 47–52.
- Yeung P.K. and Wong J.T. 2003. Inhibition of cell proliferation by mechanical agitation involves transient cell cycle arrest at G1 phase in dinoflagellates. *Protoplasma*. 220, 173–178.
- Yu X., Cai G., Wang H., Hu Z., Zheng W., Lei X., Zhu X. et al. 2018. Fast-growing algicidal *Streptomyces* sp. U3 and its potential in harmful algal bloom controls. *J. Hazard. Mater.* 341, 138–149.
- Yu Z., Song X., Cao X. and Liu Y. 2017. Mitigation of harmful algal blooms using modified

clays: theory, mechanisms, and applications. *Harmful Algae*. 69, 48–64.

Zhang F., Fan Y., Zhang D., Chen S., Bai X., Ma X., Xie Z. et al. 2020. Effect and mechanism of the algicidal bacterium *Sulfitobacter porphyrae* ZFX1 on the mitigation of harmful algal blooms caused by *Prorocentrum donghaiense*. *Environ. Pollut.* 263, 114475.

Zhang F., Ye Q., Chen Q., Yang K., Zhang D., Chen Z., Lu S. et al. 2018. Algicidal activity

of novel marine bacterium *Paracoccus* sp. strain Y42 against a harmful algal-bloom-causing dinoflagellate, *Prorocentrum donghaiense*. *Appl. Environ. Microbiol.* 84, e01015-18.

Zirbel M.J., Veron F. and Latz M.I. 2000. The reversible effect of flow on the morphology of *Ceratocorys horrida* (Peridinales, Dinophyta). *J. Phycol.* 36, 46–58.

**Address for correspondence:** Olga Matantseva. Institute of Cytology RAS, Tikhoretsky Ave. 4, 194064 St. Petersburg, Russia; e-mail: [matantseva@incras.ru](mailto:matantseva@incras.ru)