= ORIGINAL PAPERS =

The Pumping Rate of the White Sea Sponge *Halichondria panicea* (Pallas, 1766) (Porifera: Demospongiae)

V. V. Khalaman^a, * (ORCID: 0000-0001-5426-0607) and P. A. Lezin^a (ORCID: 0000-0002-6699-4162)

 ^a Zoological Institute, Russian Academy of Sciences, St. Petersburg, 199034 Russia *e-mail: VKhalaman@gmail.com
Received November 8, 2021; revised January 31, 2022; accepted March 4, 2022

Abstract—The pumping rate of the White Sea sponge *Halichondria panicea* (Pallas, 1766) (Porifera: Demospongiae) was estimated under laboratory conditions. We used live specimens with a wet weight of 3.5 to 35.5 g and one to eight oscula. The pumping rate of a sponge was determined as the sum of pumping rates of all its oscula, which was calculated as the product of the maximum velocity of the excurrent flow from an osculum by the cross-sectional area of that osculum. The velocity was measured using a microthermistor sensor. The pumping rate of the sponge was found to be related to its weight by a power relationship with an exponent of approximately 3. Sponges weighing 25 g and over surpass in pumping activity solitary animals such as the bivalves *Mytilus edulis* and *Hiatella arctica* and the ascidian *Styela rustica*, in which the relationship is either a linear or power one, with an exponent less than one. The advantage of the sponge over solitary organisms seems to be due to its modular organization, which ensures not only a constant increase in the number and size of oscula as the individual grows, but probably also leads to a periodic restructuring of the irrigation system.

Keywords: *Halichondria panicea*, pumping rate, modular organism, fouling communities, White Sea **DOI:** 10.1134/S1063074022030051

INTRODUCTION

In the North Atlantic and Pacific, the sponge *Hali-chondria panicea* (Pallas, 1766) is one of the most widespread species in epibenthic communities that form on both natural and artificial substrates [5, 10, 13, 16, 21, 29, 30]. This species of sponge is also found in the Mediterranean Sea and the Indian Ocean [24, 40].

It is known that *H. panicea* is characterized by a high growth rate [35, 48], is resistance to epibiosis [17], and has the ability to inhabit a wide range of environments, being found not only in the subtidal but also in the intertidal zone [1, 30]. In addition, H. panicea possesses toxic properties [8, 9, 12, 23], which are apparently due to symbiotic bacteria [15, 31, 44]. This suggests that *H. panicea* is a highly competitive ecologically aggressive organism. However, the competitive capacity of epibenthic organisms is not provided only by these properties. An important aspect of competitive relationships among sessile filter-feeding animals is the struggle for food [18–20, 34, 36, 50]. However, some authors believe that food competition between species in epibenthic communities is not crucial due to the excess of food in plankton or differences in food spectra [22, 37, 46]; nevertheless, this aspect of relationships should also be taken into account. The competitive abilities of filter feeders are made up of such indices as the efficiency of settling of suspended matter, its assimilation, the overlap of the food spectrum, and behavioral response characteristics. The ability to intercept water flows, which directly depends on the pumping activity of an animal, is the most important mechanism in food competition [49].

Studies of the most common species of animals that form the basis of perennial fouling communities in Kandalaksha Bay of the White Sea allowed the ranking of species in descending order of water pumping activity: the mussel Mytilus edulis, the solitary ascidian Styela rustica, and the bivalve Hiatella arctica [3]. This sequence correlates well with the position occupied by each of the species in fouling communities: the dominant species are *M. edulis* and *S. rustica*, the subdominant is *H. arctica* [6, 7]. In this work, we studied the pumping activity of the sponge H. panicea, which also plays a noticeable role in the fouling communities of the White Sea [10]. Due to the large competitive abilities of *H. panicea* [11], we assumed, as a hypothesis to be tested, that the pumping activity of H. panicea exceeds that of the mussel M. edulis and the sea squirt S. rustica; their White Sea representatives were previously assessed in terms of this index [3].

MATERIALS AND METHODS

The study was performed at the White Sea Biological Station of the Zoological Institute of the Russian Academy of Sciences, which is located in Chupa Inlet of Kandalaksha Bay of the White Sea (66°20.230' N; $33^{\circ}38.972'$ E). Test animals were collected in the vicinity of the station from fouling on ropes at a depth of 1.0–2.5 m. Sponges were carefully detached from the substrate and placed in 10-liter intensively aerated flow-through aquaria for 2 days before testing for acclimation to laboratory conditions. Natural sea water (salinity 24‰, temperature 10°C) was used. Since the pumping activity of filter-feeding organisms depends on the water temperature [14, 43], experiments with animals were carried out at a constant temperature of 10°C. A total of 20 specimens with a wet weight of 3.5 to 35.5 g and one to eight oscula were collected and tested.

The pumping rate of a sponge was determined as the sum of pumping rates of all oscula found in that specimen. The osculum pumping rate was determined as the product of the excurrent flow velocity from an osculum and the osculum cross-sectional area. The velocity of water was determined using a setup that was developed on the basis of the system for measuring fluid flow velocity [33, 42]. The principle of operation of the device is to measure the resistance of a thermistor sensor heated by direct current. The thermistor in the flow is cooled by the movement of the fluid in proportion to the flow velocity [42]. The measuring element in the device was an MT-54 microthermistor sensor (resistance 2.5 k Ω), which was incorporated in an asymmetric resistor bridge connected to the measuring device [3].

Before starting work, the device was calibrated by artificially creating water flows of different velocities. For this purpose, a set of burettes with a known flow rate was used. The obtained values of the output voltage drop (voltage difference in calm water and flow) were used to construct a calibration curve of the form:

$$V = a e^{b \Delta U},$$

where V is the velocity of water flow (mm/s); ΔU , the voltage drop (mV).

When measuring pumping activity, the sensor was placed in the center of the excurrent water flow from the osculum at a distance as close as possible to it, and at least 10 readings were sequentially recorded. The maximum value from each series of measurements was used for analysis. Based on the values of the excurrent flow velocity, the pumping rate was calculated by the formula:

$$E = \frac{VS}{1\,000\,000}$$

where *E* is the pumping rate (L/h); *V*, is the velocity of the excurrent water flow (mm/h); *S*, is the cross-sectional area of the osculum (mm²), which was calculated as the area of a circle. The diameter of each osculum was measured under a binocular loupe using an eyepiece micrometer immediately after recording the maximum velocity of the excurrent flow from that osculum. After all measurements, the wet weight of

sponges was determined by weighing on a VLKT-500 electric balance with an accuracy of 0.1 g. The animals were preliminarily dried for a while on a filter paper until the release of water had ceased.

In addition to pumping rate (E), we calculated the intensity of pumping activity (weight-specific pumping rate, I), viz., the amount of water pumped by a sponge per unit time per unit weight of that specimen. As well, we calculated the "effectiveness" indices of oscula: the relation of the pumping rate of the entire sponge to the total cross-sectional area of all oscula and the relation of weight-specific pumping rate to the total cross-sectional area of all oscula.

Mathematical processing of data was performed using the Statistica 7 (StatSoft) and OriginPro 9.0 (OriginLab) software packages. In the text and tables, the mean error serves as the index of variation of a character (if it is not specified).

RESULTS

The relationships of the total and specific pumping rates with the body weight in Halichondria panicea are best described by exponential $E(I) = ab^{W}$ or allometric (power) $E(I) = aW^b$ functions, where E is the pumping rate, L/h; I, is the specific pumping rate, L/h \times g; W, is the weight of the specimen, g; and a and b are the coefficients of the equation (Fig. 1, Table 1). However, the total and specific pumping rates were approximately the same in specimens weighing up to 20 g. These indices were significantly increased in specimens with a weight exceeding 20 g. The increase in the pumping rate of the whole sponge is due to an increase in the total oscula cross-sectional area, which is made up of an increase in the number and size of the oscula. The relationship of these parameters with the sponge weight can be described by a linear function (Fig. 2, Table 2).

Nevertheless, no general relationship between the cross-sectional area of an osculum and the maximum excurrent velocity from the osculum was found (Fig. 3). The excurrent flow velocity from the oscula varied widely from 2 to 773 mm/s and averaged 71 \pm 10 mm/s. The median (30 mm/s) was less than the mean since most oscula tested had relatively low to moderate flows. The excurrent flow velocity varied among oscula of the same specimen. For 7 out of 20 tested specimens, a statistically significant positive correlation was found between the osculum cross-sectional area and the excurrent flow velocity from the osculum (r = 0.74-0.99). The correlation was statistically insignificant for the remaining specimens; among them four had a negative correlation.

The nature of the relationship of the efficiency of oscula (the sponge pumping rate related to the crosssectional area of all oscula) and the specific efficiency of oscula (weight-specific pumping rate relative to the cross-sectional area of all oscula) with the weight of the sponge is noteworthy (Fig. 4). The former index increases with the weight of the sponge, which can best be described by a linear regression. However, the accuracy of such an approximation is not high, the coefficient of determination is only 0.32. The latter index can be considered constant, independent of the weight of the sponge. However, with an average value of 0.017 ± 0.0036 for all sponges we tested, it fluctuates within a significant range, from 0.0029 to 0.078. Perhaps, these relationships are not monotonic functions. The location of points on the graphs suggests the presence of two maxima. The first maximum was observed at a sponge weight of approximately 10 g, and the second one occurred at a weight of 30 g. For better visualization, these maxima on the graphs (Fig. 4) are described by a polynomial of the fourth degree.

The relationships between the pumping rate and body weight for filter-feeders dominating the fouling communities in the White Sea (Fig. 5) show that specimens of *H. panicea* weighing up to 15–20 g do not outperform their competitors in this characteristic, viz., the bivalves *Mytilus edulis, Hiatella arctica* and the sea squirt *Styela rustica*, which have the same or even lower body weight. However, larger sponges significantly outperform solitary filter-feeding organisms in pumping activity.

DISCUSSION

It is known that the pumping rate of sponges is variable and depends on external conditions: temperature and water current velocity [27, 41, 43]. In addition, sponges may experience a periodic short-term decrease in pumping activity that is not associated with environmental factors [32, 41]. According to the method used in our study, we recorded the maximum possible rate of pumping activity for each osculum and, consequently, for the whole sponge.

Our data contradict the statement of Kumala et al. [32] that in *Halichondria panicea* the velocity of excurrent flow from the osculum is a constant value equal to 23 ± 1.3 (confidence interval) mm/s. Our measurements show that the excurrent velocity varies from 2 to



Fig. 1. The relationship of the pumping rate (a) and the specific pumping rate (b) of the sponge *Halichondria panicea* with the body weight. Dots denote empiric data; lines are the calculated regression lines: a solid line represents an allometric (power) function and a dotted line represents an exponential function.

773 mm/s. Therefore, it can be considered constant only in the narrow sense that it does not depend on the osculum cross-sectional area (Fig. 3). In our opinion, the differences in the estimates are due to that the cited authors indirectly determined the water velocity as the ratio of the filtration rate, determined from the clearance rate, to the osculum cross-sectional area of

Species	Exponential function, $E(I) = ab^W$			Allometric (power) function, $E(I) = aW^b$			п
	A	b	<i>R</i> ²	а	b	<i>R</i> ²	
Pumping rate, E	2.6 ± 1.01	1.11 ± 0.011	0.91	0.00078 ± 0.000958	3.3 ± 0.34	0.93	20
Weight-specific pumping rate, <i>I</i>	0.19 ± 0.1066	1.08 ± 0.01	0.82	0.0009 ± 0.00121	2.3 ± 0.37	0.80	20

Table 1. The parameters of equations of nonlinear regression between the pumping rate (E, L/h)/weight-specific pumping rate $(I, L/h \times g)$ and body weight (W, g) in the sponge *Halichondria panacea*

a and b, the parameters of equations; R^2 , the coefficient of determination; n, the size of the sample.



Fig. 2. The relationship of the total cross-sectional area of oscula (a), the number of oscula (b), and the average cross-sectional area of oscula (c) with the body weight of the sponge *Halichondria panicea*. Dots denote empiric data; dotted lines represent the calculated regression lines.

sponge [32]. We performed a direct measurement of the flow velocity. It is probably also important that we used both uni- and multiosculum specimens in the experiments.

The above authors [32] conducted a study on single-osculum explants and reported a filtration rate of 0.28 ± 0.06 (confidence interval) mL/min. According to our results, such estimates of pumping activity should apply to specimens weighing approximately 2.5 g,



Fig. 3. The relationship between the osculum cross-sectional area (mm^2) and the maximum excurrent velocity from the osculum (mm/s).

which approximately corresponds to the sponge sizes reported in the cited work. When determining the excurrent velocity in single-osculum explants of H. panicea using video recording, Goldstein et al. [26] showed that the velocity varied within a fairly wide range from 5.9 to 53 mm/s, which is consistent with our data. However, these investigators found a positive relationship between the excurrent flow velocity and the osculum cross-sectional area, which is described by a power function: $U_0 = 2.59 OSA^{0.45}$ ($R^2 = 0.55$), where U_0 is the velocity of water flow, mm/s and OSA is the osculum cross-sectional area, mm². Using predominantly multiosculum specimens, we did not find convincing evidence for a relationship between these parameters. Apparently, the relationship is clear in single-osculum individuals representing a single aquiferous module, while in multi-osculum individuals it is less pronounced due to the more complex multimodule irrigation systems.

Thomassen and Riisgård [48] found that the filtration rate of *H. panicea* is described by an allometric equation: $F = 28.35 \text{DW}^{0.914}$, where F is the filtration rate, mL/min: DW, the weight of a dry sponge, g. Since the exponent is close to unity, this dependence is almost linear. According to our data, the relationship between the pumping rate and weight is also described by an allometric function, but with an exponent of approximately 3, and the function is nonlinear. For specimens with a wet weight of up to 10 g, our estimates of the filtration rate of *H. panicea* and those reported by Thomassen and Riisgård [48] are similar; however, the estimates substantially differ for sponges with a greater weight. In our opinion, in this case, this is also caused by different methodological approaches to determining sponge pumping activity. As mentioned above, the estimates we obtained reflect the maximum possible pumping rate of a sponge. Thomassen and Riisgård [48] assessed pumping activity from the water clearance rate. With this method of estimation, the result only reflects the operation of the sponge's irrigation system for a fixed period of time. However, during testing, some oscula may be inactive due to their intrinsic property to periodically open and close, including in response to various external influences [28, 43]. The greater the number of oscula is in a sponge, the higher the likelihood of underestimating results is. In addition, assessment of sponge pumping activity from water clearance rate depends on the quality of particles used for this purpose; hence, this method has been criticized [25].

As noted above, Goldstein et al. [26] determined the excurrent velocity from the osculum using video recording, which can be considered a direct measuring method. However, these authors calculated a linear relationship between the pumping rate and the volume of a single-osculum sponge *H. panicea*: $F \approx 2.3 \times V_s$, where *F* is pumping rate, mL/min; and V_s , the volume of the sponge, cm³. This contradicts the results of our studies, indicating a power or allometric dependence. The reason for the discrepancy is as follows. The relationship we obtained between the average cross-sec-



Fig. 4. The relationship of the effectiveness of oscula. (a) The pumping rate relative to the total cross-sectional area of all oscula, (b) weight-specific pumping rate of sponge relative to the total area of all oscula. Dots denote empiric data; lines represent the calculated regression lines: a solid line represents a linear relationship; a dotted line represents a polynomial of the fourth degree.

Table 2. The parameters of the equation of linear regression (y = a + bx) of the number of oscula (N_{os}) and the average cross-sectional area of an osculum (S_{os}) and the total (S) cross-sectional area of oscula on the body weight of the sponge *Halichondria panacea*

Species	A	b	R^2	п
Nos	2.5 ± 0.57	0.14 ± 0.028	0.57	20
Sos	3.2 ± 3.33	0.7 ± 0.17	0.47	20
S	-30 ± 16	6.1 ± 0.79	0.77	20
			2	

a and b, the parameters of the equation; R^2 , the coefficient of determination; n, the size of the sample.

tional area of oscula and the sponge weight is linear, while Goldstein et al. [26] describe it as being parabolic: $OSA = 1.31 \times V_s^{0.66}$, where OSA is the osculum area (mm²) and V_s is the sponge volume (cm³). This is what determines the linear nature of the relationship they obtained between sponge volume and pumping activity. We performed calculations using the data from Goldstein et al. [26]. The relationship between oscula area and sponge volume is better described by a linear function: $OSA = 1.33 \times V_s + 0.19$. The coefficient of determination for a linear function is 0.83, while for a parabolic one it is 0.66. It only remains to wonder why the above authors used the parabolic function. Most likely this is due to the fact that it well suited to the theoretical constructions of the authors that are related to the arrangement of the choanocyte chambers in the sponge H. panicea (see: [26]). It should be noted that a study performed on 20 species of both uni- and multiosculum Demospongiae (see: [39]) showed that the sponge volume and the area of oscula are allometrically related, with an exponent of 0.6 to 1.0 in different species. It is possible that the mathematical model proposed by Goldstein et al. [26] works satisfactorily within single-osculum specimens, but it is unsuitable for specimens of *H. panacea* with multiple oscula. Undoubtedly, single-osculum explants



Fig. 5. The relationship of the pumping rate of *Mytilus edulis*, *Styela rustica*, *Hiatella arctica* [3], and *Halichondria panicea* with the body weight of the animal.

of *H. panicea* provide a relatively simple and convenient biological model for studying the filtration activity of sponges; however, the findings obtained on single-osculum specimens cannot be completely extrapolated to animals with multiple oscula.

As follows from a comparison of the pumping activity of fouling animals (Fig. 5), specimens of *H. panicea* weighing less than 15 g have moderate pumping rates, while those weighing 25 g and more surpass the largest mussels in this index and are thus beyond competition in shallow water fouling communities in the White Sea. Specimens weighing 40 g pump water at a rate of approximately 150 liters per hour. This powerful pumping activity, along with toxicity [8, 9, 12, 23, 31] and high somatic growth rates [16, 48], probably contributes to the high competitive ability of *H. panicea* [11].

The superiority of *H. panicea* over its competitors in terms of water pumping is due to the fact that this characteristic and the body weight of the sponge are related by a power function with an exponent greater than unity. In the bivalves *Mytilus edulis* and *Hiatella arctica* and the ascidian *Styela rustica*, the same relationship is described by functions with an exponent less than unity [45, 47] or equal to unity [3]. The peculiarity of *H. panicea* can be explained by its modular organization giving the sponge advantages over solitary organisms, in which the development of the filtration apparatus is limited [2, 38].

As the sponge grows, not only do the number and the average and total cross-sectional area of oscula increase; the sponge irrigation system is apparently also periodically restructured. The reorganization occurs when the system performance reaches a maximum. This is indicated by the nature of the relationship between the "effectiveness" of oscula and the sponge weight, which, in contrast to the number/total cross-sectional area of oscula relationship (Fig. 2), is not a monotonic function but is a change of minima and maxima (Fig. 4). Our data suggest that the reorganization of the irrigation system occurs in those H. panicea that have attained a weight of approximately 20 g. Of course, this hypothesis requires further verification. However, when analyzing the morphometric parameters of the White Sea sponge Polymastia mammillaris, Plotkin et al. [4] came to a similar conclusion: "It seems that, as it grows, P. mammillaris can solve the problems of internal hydrodynamics both by increasing the number of irrigation modules and by improving the irrigation system of the existing modules" ([4], pp. 25–26).

FUNDING

The study was supported by a grant no. 20-54-15002 NTsNI_a from the Russian Foundation for Basic Research and by the State Assignment Project no. 1021051402749-2.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflicts of interest.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

REFERENCES

- Ereskovsky, A.V., Some patterns of habitats and distribution of sponges in the littoral zone of Eastern Murman, *Zool. Zh.*, 1994, vol. 73, no. 4, pp. 5–17.
- Ereskovskii, A.V., Problems of coloniality, modularity, and individuality in sponges and special features of their morphogeneses during growth and asexual reproduction, *Russ. J. Mar. Biol.*, 2003, vol. 29, pp. S46–S56.
- Lezin, P.A., Agat'eva, N.A., and Khalaman, V.V., A comparative study of the pumping activity of some fouling animals from the White Sea, *Russ. J. Mar. Biol.*, 2006, vol. 32, no. 4, pp. 245–249.
- Plotkin, A.S., Ereskovsky, A.V., and Khalaman, V.V., The analysis of modular organization of Porifera using the White Sea sponge *Polymastia mammillaris* (Muller, 1806) (Demospongiae, Tetractinomorpha) as a model, *Zh. Obshch. Biol.*, 1999, vol. 60, no. 1, pp. 26–28.
- Plotkin, A.S., Railkin, A.I., Gerasimova, E.I., et al., Subtidal underwater rock communities of the White Sea: Structure and interaction with bottom flow, *Russ. J. Mar. Biol.*, 2005, vol. 31, no. 6, pp. 335–343.
- 6. Oshurkov, V.V., Suktsessii i dinamika epibentosnykh soobshchestv verkhnei sublitorali boreal'nykh vod (Successions and Dynamics of Epibenthic Communities from the Boreal Upper Subltidal Zone), Vladivostok: Dal'nauka, 2000.
- Khalaman, V.V., Fouling communities of mussel aquaculture installations in the White Sea, *Russ. J. Mar. Biol.*, 2001, vol. 27, no. 4, pp. 227–237.
- Khalaman, V.V., Belyaeva, D.V., and Flyachinskaya, L.P., Effect of excretory-secretory products of some fouling organisms on settling and metamorphosis of the larvae of *Styela rustica* (Ascidiae), *Russ. J. Mar. Biol.*, 2008, vol. 34, no. 3, pp. 170–173.
- Khalaman, V.V., Korchagina, N.M., and Komendantov, A.Yu., The impact of waterborne cues from conspecifics and other species on the larvae of *Halichondria panacea* Pallas, 1766 (Porifera: Demospongiae), *Russ. J. Mar. Biol.*, 2014, vol. 40, no. 1, pp. 36–42.
- Khalaman, V.V. and Komendantov, A.Yu., Structure of fouling communities formed by *Halichondria panicea* (Porifera: Demospongiae) in the White Sea, *Russ. J. Ecol.*, 2011, vol. 42, 493.
- Khalaman, V.V. and Komendantov, A.Yu., Experimental study of the ability of the sponge *Halichondria panicea* (Porifera: Demospongiae) to compete for a substrate in shallow-water fouling communities of the White Sea, *Biol. Bull. Russ. Acad. Sci.*, 2016, vol. 43, no. 1, pp. 69–74.

- Khalaman, V.V., Sharov, A.N., Kholodkevich, S.V., et al., Influence of the White Sea sponge *Halichondria panicea* (Pallas, 1766) on physiological state of the blue mussel *Mytilus edulis* (Linnaeus, 1758), as evaluated by heart rate characteristics, *J. Evol. Biochem. Physiol.*, 2017, vol. 53, no. 3, pp. 225–232.
- Khodakovskaya, A.V., Fauna of sponges (Porifera) of Peter the Great Bay, Sea of Japan, *Russ. J. Mar. Biol.*, 2005, vol. 31, no. 4, pp. 209–214.
- Chernyaev, M.Zh., Rodionov, I.A., and Selin, N.I., Water-pumping activity of the mussel *Mytilus trossulus* under different living conditions, *Russ. J. Mar. Biol.*, 1998, vol. 24, no. 2, pp. 131–133.
- Althoff, K., Schütt, C., Steffen, R., et al., Evidence for a symbiosis between bacteria of the genus *Rhodobacter* and the marine sponge *Halichondria panicea*: Harbor also for putatively toxic bacteria?, *Mar. Biol.*, 1998, vol. 130, pp. 529–536.
- Barthel, D., On the ecophysiology of the sponge *Hali-chondria panicea* in Kel Bight. I. Substrate specificity, growth and reproduction, *Mar. Ecol.: Prog. Ser.*, 1986, vol. 32, pp. 291–298.
- Barthel, D. and Wolfrath, R., Tissue sloughing in the sponge *Halichondria panicea*: A fouling organism prevents being fouled, *Oecologia*, 1989, vol. 78, pp. 357– 360.
- Comeau, L.A., Filgueira, R., Guyondet, T., and Sonier, R., The impact of invasive tunicates on the demand for phytoplankton in longline mussel farms, *Aquaculture*, 2015, vol. 441, pp. 95–105.
- Daigle, R.M. and Herbinger, C.M., Ecological interactions between the vase tunicate (*Ciona intestinalis*) and the farmed blue mussel (*Mytilus edulis*) in Nova Scotia, Canada, *Aquat. Invasions*, 2009, vol. 4, no. 1, pp. 177–187.
- Dalby, J.E. and Young, C.M., Variable effects of ascidian competitors on oysters in a Florida epifaunal community, *J. Exp. Mar. Biol. Ecol.*, 1993, vol. 167, no. 1, pp. 47–57.
- Dijkstra, J., Sherman, H., and Harris, L.G., The role of colonial ascidians in altering biodiversity in marine fouling communities, *J. Exp. Mar. Biol. Ecol.*, 2007, vol. 342, no. 1, pp. 169–171.
- Dubois, S., Orvain, F., Marin-Léal, J.C., et al., Small-scale spatial variability of food partitioning between cultivated oysters and associated suspension-feeding species, as revealed by stable isotopes, *Mar. Ecol.: Prog. Ser.*, 2007, vol. 336, pp. 151–160.
- Dyrynda, P.E.J., Modular sessile invertebrates contain larvotoxic allelochemicals, *Dev. Comp. Immunol.*, 1983, vol. 7, no. 4, pp. 621–624.
- Erpenbeck, D., Knowlton, A.L., Talbot, S.L., et al., A molecular comparison of Alaskan and North East Atlantic *Halichondria panicea* (Pallas 1766) (Porifera: Demospongiae) populations, *Boll. Mus. Ist. Biol. Univ. Genova*, 2004, vol. 68, pp. 319–325.

- Frost, T.M., In situ measurements of clearance rates for the freshwater sponge *Spongilla lacustris, Limnol. Oceanogr.*, 1978, vol. 23, no. 5, pp. 1034–1039.
- Goldstein, J., Riisgård, H.U., and Larsen, P.S., Exhalant jet speed of single-osculum explants of the demosponge *Halichondria panicea* and basic properties of the sponge-pump, *J. Exp. Mar. Biol. Ecol.*, 2019, vol. 511, pp. 82–90.
- Hadas, E., Ilan, M., and Shpigel, M., Oxygen consumption by a coral reef sponge, *J. Exp. Biol.*, 2008, vol. 211, no. 13, pp. 2185–2190.
- Hartman, W.D. and Reiswig, H.M., The individuality of sponges, in *Animal Colonies*, Boardman, R.S., Cheetham, A.H., and Oliver, W.A., Eds., Stroudsburg: Dowden, Hutchinson and Ross, 1973, pp. 567–584.
- 29. Hoare, R. and Peattie, M.E., The sublittoral ecology of the menai strait: I. Temporal and spatial variation in the fauna and flora along a transect, *Estuarine Coastal Mar. Sci.*, 1979, vol. 9, no. 6, pp. 663–675.
- Knowlton, A.S. and Highsmith, R.C., Convergence in the time-space continuum: A predator-prey interaction, *Mar. Ecol.: Prog. Ser.*, 2000, vol. 197, pp. 285–291.
- Kobayashi, M. and Kitagawa, I., Likely microbial participation in the production of bioactive marine sponge chemical constituents, in *Sponge Sciences: Multidisciplinary Perspectives*, Tokyo: Springer, 1998, pp. 379–389.
- 32. Kumala, L., Riisgard, H.U., and Canfield, D.E., Osculum dynamics and filtration activity in small single-osculum explants of the demosponge *Halichondria panicea, Mar. Ecol.: Prog. Ser.*, 2017, vol. 572, pp. 117–128.
- LaBarbera, M. and Vogel, S., An inexpensive thermistor flow meter for aquatic biology, *Limnol. Oceanol.*, 1976, vol. 21, no. 5, pp. 750–756.
- Leblanc, A.R., Landry, T., and Miron, G., Fouling organisms of the blue mussel *Mytilus edulis*: Their effect on nutrient uptake and release, *J. Shellfish Res.*, 2003, vol. 22, no. 3, pp. 633–638.
- Leichter, J.J. and Witman, J.D., Water flow over subtidal rock walls: Relation to distributions and growth rates of sessile suspension feeders in the Gulf of Maine Water flow and growth rates, *J. Exp. Mar. Biol. Ecol.*, 1997, vol. 209, nos. 1–2, pp. 293–307.
- Lesser, M.P., Shumway, S.E., Cucci, T., and Smith, J., Impact of fouling organisms on mussel rope culture: Interspecific competition for food among suspension-feeding invertebrates, *J. Exp. Mar. Biol. Ecol.*, 1992, vol. 165, no. 1, pp. 91–102.
- Lohse, D.P., Relative strengths of competition for space and food in a sessile filter feeder, *Biol. Bull.*, 2002, vol. 203, no. 2, pp. 173–180.
- Marfenin, N.N., Sponges viewed in the light of up-todate conception on coloniality, *Berl. Geowiss. Abh., Reihe E*, 1997, vol. 20, pp. 17–23.
- Morganti, T.M., Ribes, M., Moskovich, R., et al., *In* situ pumping rate of 20 marine Demosponges is a function of osculum area, *Front. Mar. Sci.*, 2021, vol. 8, 583188.

- 40. Purushottama, G.B., Venkateshvaran, K., Pani Prasad, K., and Nalini, P., Bioactivities of extracts from the marine sponge *Halichondria panicea, J. Venomous Anim. Toxins Incl. Trop. Dis.*, 2009, vol. 15, no. 3, pp. 444–459.
- 41. Reiswig, H.M., *In situ* pumping activities of tropical Demospongiae, *Mar. Biol.*, 1971, vol. 9, pp. 38–50.
- Riedl, R.J. and Machan, R., Hydrodynamic patterns in lotic intertidal sands and their bioclimatological implications, *Mar. Biol.*, 1972, vol. 13, pp. 179–209.
- 43. Riisgård, H.U., Kumala, L., and Charitonidou, K., Using the F/R-ratio for an evaluation of the ability of the demosponge *Halichondria panicea* to nourish solely on phytoplankton versus free-living bacteria in the sea, *Mar. Biol. Res.*, 2016, vol. 12, no. 9, pp. 907–916.
- 44. Schneemann, I., Nagel, K., Kajahn, I., et al., Comprehensive investigation of marine *Actinobacteria* associated with the sponge *Halichondria panicea*, *Appl. Environ. Microbiol.*, 2010, vol. 76, no. 11, pp. 3702–3714.
- 45. Sejr, M.K., Petersen, J.K., Jensen, K.T., and Rysgaard, S., Effects of food concentration on clearance rate and energy budget of the Arctic bivalve *Hiatella arctica* (L) at subzero temperature, *J. Exp. Mar. Biol. Ecol.*, 2004, vol. 311, no. 1, pp. 171–183.

- Stuart, V. and Klumpp, D.W., Evidence for food-resource partitioning by kelp-bed filter feeders, *Mar. Ecol.: Prog. Ser.*, 1984, vol. 16, pp. 27–37.
- Sukhotin, A.A., Lajus, D.L., and Lesin, P.A., Influence of age and size on pumping activity and stress resistance in the marine bivalve *Mytilus edulis* L., *J. Exp. Mar. Biol. Ecol.*, 2003, vol. 284, nos. 1–2, pp. 129–144.
- Thomassen, S. and Riisgård, H.U., Growth and energetics of the sponge *Halichondria panicea, Mar. Ecol.: Prog. Ser.*, 1995, vol. 128, pp. 239–246.
- 49. Troost, K., Stamhuis, E.J., van Duren, L.A., and Wolff, W.J., Feeding current characteristics of three morphologically different bivalve suspension feeders, *Crassostrea gigas, Mytilus edulis* and *Cerastoderma edule*, in relation to food competition, *Mar. Biol.*, 2009, vol. 156, no. 3, pp. 355–372.
- Zajac, R.N., Whitlatch, R.B., and Osman, R.W., Effects of inter-specific density and food supply on survivorship and growth of newly settled benthos, *Mar. Ecol.: Prog. Ser.*, 1989, vol. 56, no. 1, pp. 127–132.

Translated by T. Koznova