 Polar Record 49 (250): 272–277 (2013). doi:10.1017/S0032247412000629

Modifications of gill lipid composition in littoral and cultured blue mussels *Mytilus edulis* L. under the influence of ambient salinity

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ABSTRACT. Changes of the lipid composition (mainly of membrane lipids) in gills in response to various seawater salinities were studied in two groups of mussels *Mytilus edulis* L. from the White Sea, living under different environmental conditions (intertidal zone and artificial substrates used in aquaculture). Modifications in the lipid composition involved the basic indices characteristic of the physical state of biological membranes, and minor components of the lipid bilayer, which perform regulatory functions, indicating that the lipid metabolism of the bivalves has undergone acclimation transformations in response to salinity. It is demonstrated that the response to critical salinity (5 ppt) in membrane lipids was similar in the two investigated groups of mussels, whereas with salinities of 15, 35, and 45 ppt the pattern of fluctuations in the lipid composition depended on the initial habitat (intertidal zone or aquaculture).

Introduction

Modifications in the lipid composition, especially in the membrane fractions, represent a key biochemical adaptation of marine organisms to various environmental stresses (Hochachka and Somero 1984; Thompson 1986; Gibbs 1998; Logue and others 2000; Los and Murata 2004). The cell membrane is among the first components to be affected by the different environmental factors, such as temperature or salinity. These impacts lead to alterations in the physical properties of the membrane lipids. Changes in the lipid bilayer fluidity, a principal characteristic of the physical state of the membrane, facilitate stabilisation of membrane permeability, as well as normal function of ion channels, enzymes and receptors. Modifications in the membrane lipids have been shown to return the physical state of the membranes toward that existing prior to imposition of the stress (Thompson 1986). A primary compensatory response to stress is the change in the degree of unsaturation of phospholipid fatty acids, expressed as a saturated/polyunsaturated fatty acid ratio (SFA/PUFA). Quantitative changes in the main lipid classes (ratios such as phosphatidylethanolamine (PE)/phosphatidylcholine (PC) and cholesterol/phospholipids) represent secondary adjustments to initial lipid changes under stress (Thompson 1986). For instance, the induction by low temperatures of the synthesis of unsaturated fatty acids to compensate for presumed decrease in membrane fluidity is a widespread phenomenon called 'homeoviscous acclimation' (Sinensky 1974; Los and Murata 2004). Salinity, along with other abiotic environmental factors, is a central factor influencing the physiological functions of marine organisms living in the intertidal zone, where salinity variations are pronounced. It has been assumed that hyperosmotic stress, like low temperature, leads to reduced membrane fluidity, whereas hypoosmotic stress (desalination of the medium) is presumed to cause opposite modifications in the physical state of membranes (Los and Murata 2004).

The blue mussel *Mytilus edulis* L. is a typical sedentary, osmoconformer, bivalve mollusc. During environmental salinity changes, mussels achieve intracellular osmotic balance by the accumulation or loss of both organic and inorganic solutes. Mussels demonstrate a number of behavioural, physiological, biochemical and molecular responses when exposed to different salinities of seawater (Berger 1986; Fokina and others 2006; Bondareva and others 2006; Fokina and others 2007; Vysotskaya and Nemova 2008; Fokina and others 2010).

This study investigated two groups of White Sea mussels living under different conditions: (1) littoral (intertidal) mussels, which inhabit a fluctuating environment (periodic impact of tidal cycles, spring–autumn desalinations, wave activity, temperature differences and other factors); (2) cultured mussels raised under fairly steady conditions on suspended substrates. These two groups of mussels are assumed to employ different mechanisms of acclimation at the lipid composition level in response to changes in salinity. Here, the lipid composition in the gills of White Sea mussels is studied. This organ in bivalves is often exposed to environmental impact and is sensitive to the action of various factors (Avery and others 1998).

Materials and methods

The study object was a bivalve mollusc, a typical inhabitant of the White Sea littoral zone: the blue mussel, *Mytilus edulis* L. (1758). Sampling and experiments were carried out at the Kartesh Biological Research Station of the Russian Academy of Science Zoological Institute (Chupa Bay, Gulf of Kandalaksha, White Sea) in August 2006. Cultured mussels (aged three years or older, with shell length 35–50mm) were collected from artificial

substrates of experimental aquaculture from a depth of 1.5–2.5m. Littoral animals (aged eight years or older, with shell length 42–45 mm) were collected from the mid intertidal zone. After encrusted organisms had been cleaned off the shells, the animals were acclimatised to laboratory conditions for several days. One week proved to be sufficient for blue mussels to acclimatise to the new conditions (Bakhmet and others 2005). The molluscs (15 cultured mussels and 20–25 littoral mussels) were kept in plexiglas tanks (20 litres) with aerated seawater with a salinity of 25 ppt under constant light and at a temperature of 10°C. The water was partially replaced on a daily basis. The animals were kept without feeding to avoid specific dynamic action. During the experiment, the two groups of mussels were kept in aquaria containing water with a salinity of 5, 15, 25, 35 and 45 ppt for 14 days. The salt concentration of 25 ppt was set as the control in the experiment, since this was the salinity in the sampling sites. A decreased salt content was produced by dilution with distilled water, while salt content was increased by addition of synthetic sea salt (Instant Ocean, USA). After the experimental exposure period was over, the mussel gills 500 mg ($n = 9$) were fixed in 96% ethanol for further analysis. Lipids were extracted after Folch and others (1957). Quantitative content of total phospholipids was determined by the hydroxamate method (Sidorov and others 1972), and cholesterol by the staining reaction (Engelbrecht and others 1974). The methyl esters of fatty acids were separated by gas-liquid chromatography using the Chromatek-Kristall-5000.1 system (Russia). Fractional analysis of individual phospholipid fractions was performed by high-performance liquid chromatography (HPLC) (Stayer, Russia) after Arduini and others (1996).

Statistical differences between the control and experimental groups were determined by the Mann-Whitney U-test and one- and two-way analysis of variance (ANOVA) tests. Statistical significance was accepted at $P < 0.05$.

Results and discussion

Comparative analysis of some membrane lipids and their fatty acids in blue mussels from two habitats, intertidal (frequent salinity fluctuations) and aquaculture (stable) showed (Tables 1, 2) that littoral *Mytilus edulis* contained higher concentrations of cholesterol, saturated fatty acids (SFA) and n-6 polyunsaturated fatty acids (PUFA, polyenes), whereas cultured mussels contained higher concentrations of n-3 polyunsaturated fatty acids and 22 non-methylene interrupted fatty acids (NMIFA). The gills of intertidal mussels had an increased content of membrane components stabilising the lipid bilayer (cholesterol and SFA) and n-6 PUFA, which due to their physical properties leads to optimal membrane permeability and regulates the activity of membrane-bound proteins (Vance and Vance 2002). We presume this adaptation is needed for the tolerance and survival of littoral mussels under frequent environment fluctuations (such as temperature and salinity). The fatty acid composition of cultured blue mussels is noted for high content of n-3 PUFA, represented predominantly by eicosapentanoic 20:5n-3 and docosahexanoic 22:6n-3 acids. That is presumably due to greater access to phytoplanktonic food. It is known that phytoplankton represents the largest food source for bivalve molluscs and contains a high proportion of these fatty acids (Ackman and others 1974; Freites and others 2002). However, increased concentration of 22 NMIFA in the gills of cultured mussels in comparison with intertidal mussels indicates activation of their metabolism in the absence of food in laboratory conditions.

Seawater desalination to 15 ppt caused an increase compared to the control (25 ppt) in the total phospholipids content in the lipid composition of intertidal mussel gills, mainly owing to the basic membrane fraction PC, as well as the minor phospholipid phosphatidylserine (PS) (Table 1). A reduction in the proportion of cholesterol in the gill membranes (low cholesterol/phospholipids ratio) suggested the membrane bilayer structure had gained fluidity in response to desalination of the seawater. In cultured mussels, on the contrary, a rise in the concentration of membrane phospholipids (namely PC, PE and PS) was accompanied by a significant increase in the concentration of SFA (the level of n-3 PUFA falling markedly) (Table 2), indicating a compensatory response developed at the membrane lipid level to stabilise the structure of the lipid bilayer in gills under the destabilising effect of low seawater salinity.

Under salinity reduction to 5 ppt littoral mussels demonstrated a substantial decrease in total phospholipids concentration, which affected the cholesterol/phospholipids ratio (Table 1), indicating that the main stabilising component, cholesterol, prevailed in gill membranes. Some phospholipid fractions showed a reduction in PC, a dominant membrane phospholipid, while the ratio of membrane phospholipids PE/PC (Table 1) shifted towards PE dominance in the membrane bilayer. There was a decrease in the concentration of saturated fatty acids (which stabilise the bilayer structure) and a rise in the concentration of n-3 and n-6 polyenes (increase the bilayer fluidity) in intertidal mussel gills (Table 1). Furthermore, among PUFA the ratio of n-3/n-6 acids shifted towards n-6 polyenes, mainly arachidonic 20:4n-6 acid, suggesting that seawater desalination to 5 ppt leads to activation of biosynthesis of essential arachidonic acid and development of compensatory modifications in the fatty acid metabolism. Arachidonic acid is actively utilised in the synthesis of eicosanoids, biologically active molecules that participate in molecular adaptations of animals to various impacts (Freas and Grollman 1980; Stanley-Samuelson 1987; Di Marzo and others 1991). Interestingly, cultured mussels *Mytilus edulis*, which were living under stable conditions, namely the absence of periodic rises and falls of seawater salinity, demonstrated similar modifications in the gill membrane lipids, that is, increase in cholesterol concentration, and hence increase in PE/PC ratio (Table 2) and a shift in n-3/n-6 PUFA ratio towards n-6 polyenes, owing to a significant increase

Table 1. Content of some basic membrane lipids (% dry weight) and fatty acids of total lipids (% total fatty acids) in the gills of littoral mussels acclimated to various salinities. Statistical differences between the control (25 ppt) and experimental groups (5, 15, 35 and 45 ppt) were determined by the Mann-Whitney U-test (*) and one-way ANOVA test (ˇ). The two-way ANOVA test (') was used in the comparison of littoral and cultured mussels under different salinities. Statistical significance was accepted at $P<0.05$.

Salinity (ppt)	5	15	25 (cont)	35	45
Phospholipids	2.08ˇ*	8.73ˇ*'	5.75	5.03	6.48'
Cholesterol	8.28'	6.45	7.75'	5.86	5.13ˇ*
Cholesterol/phospholipids	4.17ˇ*'	0.74ˇ*	1.40	1.20	0.84*
Phosphatidylinositol	0.04ˇ*'	0.02*	0.00'	0.20ˇ*	0.02ˇ*'
Phosphatidylserine	0.11'	0.25*	0.11	0.14	0.17ˇ*'
Phosphatidylethanolamine	0.12	0.45	0.23	0.24	0.29
Phosphatidylcholine	0.39ˇ*	5.56ˇ*	3.23	2.72	3.73
Lysophosphatidylcholine	0.28ˇ*	1.18'	1.23'	0.76ˇ*	1.37'
Sphingomyelin	0.09ˇ*	0.02*'	0.01	0.02	0.02
Phosphatidylethanolamine/ phosphatidylcholine	0.32ˇ*'	0.08	0.07'	0.09*	0.08
Fatty acids of total lipids					
16:0	10.82	15.07	11.84	14.20	12.23
18:0	3.23ˇ*	4.41ˇ*	7.93	4.98ˇ*	5.27
Total saturated fatty acids	18.56ˇ*	23.41	24.47'	23.70	19.93ˇ
16:1(n-7)	6.60ˇ*'	6.04	4.21	4.67	2.76*
18:1(n-9)	2.72ˇ*	4.61	4.03	4.05'	3.25*
18:1(n-7)	1.46ˇ*'	1.73*'	3.85'	1.33*	1.55*
20:1(n-9)	2.96ˇ*	3.15ˇ*	1.80	4.10ˇ*'	3.72ˇ*'
20:1(n-7)	0.60ˇ*'	0.80ˇ*'	0.39'	0.79ˇ*	0.67ˇ*
Total monounsaturated fatty acids	20.83'	23.12'	21.45	22.40'	18.61
16:4(n-3)	1.02ˇ*	0.52	0.32	1.50	2.69*
18:3(n-3)	0.51	0.73	0.57	0.56	0.50
20:2(n-3)	0.76	0.79	0.95	1.27	0.71
20:4(n-3)	0.24*	0.36	0.35	0.25'	0.22*'
20:5(n-3)	10.31'	9.22'	9.52'	9.21	10.35
22:5(n-3)	0.91ˇ*	0.84ˇ*	1.11	0.77*	1.07
22:6(n-3)	14.31'	11.96'	13.25'	12.82'	15.75'*
Total n-3 polyunsaturated fatty acids	28.79'	25.60'	27.04'	26.73'	33.24'
18:2(n-6)	1.28'	1.34'	1.38'	1.18ˇ*'	1.17ˇ*'
20:2(n-6)	0.46'	0.36'	0.36'	0.41'	0.42'
20:4(n-6)	8.26ˇ*'	6.39'	6.34'	6.36'	7.02ˇ*'
22:4(n-6)	0.93ˇ*'	1.02	0.78'	0.90'	0.94
22:5(n-6)	0.91'	1.83	0.90'	0.73ˇ*'	0.93
Total n-6 polyunsaturated fatty acids	13.96ˇ'*	12.61'	11.46'	11.32'	12.60ˇ*'
20 non-methylene interrupted fatty acids	8.10ˇ*'	5.93'	6.24	6.67'	5.82ˇ*'
22 non-methylene interrupted fatty acids	7.74ˇ*'	6.19'	6.45'	6.39'	7.05'
Total polyunsaturated fatty acids	42.75ˇ*'	38.21'	38.50'	38.05'	45.84ˇ*
Saturated fatty acids/polyunsaturated fatty acids	0.43ˇ*	0.61'	0.64'	0.62	0.43ˇ*
n-3/n-6	2.06ˇ'	2.03*'	2.36'	2.36'	2.64'
20:4n-6/18:2n-6	6.44ˇ*'	4.93	4.63'	5.37	6.03ˇ*

in the concentration of arachidonic acid (Table 2). In littoral and cultured mussel gills, changes were observed in 20 and 22 NMIFA and monounsaturated fatty acids (MUFA, monoenes), precursors for their synthesis, such as 16:1n-7, 18:1n-9, 18:1n-7, 20:1n-9 and 20:1n-7. This indicates that desalination to 5 ppt activates synthesis not only of n-3 and n-6 families polyenes but also of fatty acids with isolated double bounds, NMIFA, which are known to make cell membranes more resistant to oxidative processes and microbial lipases than common PUFA (Zhukova 1991; Barnathan 2009). Moreover, 22 NMIFA content in cultured mussels that live in a stable environment (not affected by seasonal salinity fluctuations) correlated with the deficiency of essential n-3 PUFA, whereas in the gills of littoral mussels n-3 and n-6 PUFA and NMIFA content increased simultaneously. Salinity of 5‰ is considered critical for most marine molluscs (Khlebovich 1974; Berger 1986). In the present study the experimental mussels (under 5 ppt salinity) demonstrate a typical non-specific adaptive mechanism of isolation from the environment (shell valves were kept closed during the whole exposure period), turn to the anaerobic pathways of metabolism, reduction of total metabolism and so on. Thus, the similar response of intertidal and cultured mussels' gill membrane lipids and fatty acids of total lipids can be regarded as a non-specific reaction of the lipid metabolism to prolonged anaerobic conditions induced by extreme desalination of seawater.

Ambient salinity increased to 35 ppt (versus 25 ppt in the control) leads to compensatory modifications in the

https://doi.org/10.1017/S0032247412000629 Published online by Cambridge University Press

Table 2. Content of some basic membrane lipids (% dry weight) and fatty acids of total lipids (% total fatty acids) in the gills of cultured mussels acclimated to various salinities. Statistical differences between the control (25ppt) and experimental groups (5, 15, 35 and 45ppt) were determined by the Mann-Whitney U-test (*) and one-way ANOVA test (ˇ). The two-way ANOVA test (') was used in the comparison of littoral and cultured mussels under different salinities. Statistical significance was accepted at $P<0.05$.

Salinity (ppt)	5	15	25 (cont)	35	45
Phospholipids	4.21	7.75ˇ*	4.10	5.39	4.74'
Cholesterol	7.43ˇ*'	7.46	5.68'	8.62	5.10
Cholesterol/phospholipids	1.84'	1.01	1.47	1.62	1.16
Phosphatidylinositol	0.09ˇ*'	0.03ˇ*	0.01'	0.13ˇ*	0.02'
Phosphatidylserine	0.19ˇ'	0.21ˇ*	0.08	0.14*	0.14ˇ*'
Phosphatidylethanolamine	0.19	0.44ˇ*	0.19	0.24	0.24
Phosphatidylcholine	1.33ˇ*	5.33ˇ*	2.33	2.81	3.17
Lysophosphatidylcholine	0.50	0.33'	0.49'	1.00	0.74'
Sphingomyelin	0.14ˇ*	0.06ˇ*'	0.02	0.03	0.02
Phosphatidylethanolamine/ phosphatidylcholine	0.14ˇ*'	0.08	0.08'	0.09	0.07
Fatty acids of total lipids					
16:0	13.06ˇ	13.10ˇ*	11.43	11.99	13.31ˇ*
18:0	3.86	7.19	5.20	8.04	6.46
Total saturated fatty acids	20.42	24.22ˇ*	19.08'	24.98ˇ*	23.12
16:1(n-7)	5.88ˇ*'	4.41	3.49	4.02	4.53
18:1(n-9)	3.50	3.34	2.95	2.83'	3.15
18:1(n-7)	1.06ˇ*'	1.58'	1.68'	1.93	1.72
20:1(n-9)	2.95ˇ*	3.32ˇ*	1.57	1.84ˇ'	2.92ˇ*'
20:1(n-7)	1.00ˇ*'	0.94ˇ*'	0.65'	0.67	0.96
Total monounsaturated fatty acids	20.20ˇ*'	20.76ˇ*'	17.98	17.92'	20.78ˇ*
16:4(n-3)	0.59ˇ	0.26ˇ*	3.88	0.40*	0.78
18:3(n-3)	0.42	0.26*	0.63	0.53	0.43
20:2(n-3)	0.74ˇ*	0.87ˇ*	1.38	1.20	0.85ˇ*
20:4(n-3)	0.17	0.42	0.29	0.22'	0.24'
20:5(n-3)	12.54'	11.47'	13.05'	11.58	11.69
22:5(n-3)	1.06	1.05	1.02	1.10*	1.20ˇ*
22:6(n-3)	17.07ˇ*'	14.68'	15.57'	15.51'	14.76
Total n-3 polyunsaturated fatty acids	33.00ˇ*'	31.03ˇ*'	37.26'	30.94ˇ*'	31.59ˇ*
18:2(n-6)	0.83'	0.87'	0.92'	1.09'	0.87'
20:2(n-6)	1.08'	1.36'	1.20'	1.31'	1.28'
20:4(n-6)	5.62ˇ*'	4.79'	5.22'	4.80ˇ*'	4.30ˇ*'
22:4(n-6)	0.60ˇ*'	0.79ˇ*	0.44'	0.54'	1.32*
22:5(n-6)	0.57'	0.64	0.58'	0.63'	1.10ˇ
Total n-6 polyunsaturated fatty acids	10.74ˇ*'	10.03'	10.30'	10.38'	10.47'
20 non-methylene interrupted fatty acids	5.66'	5.85'	5.69	5.96'	5.35'
22 non-methylene interrupted fatty acids	8.61ˇ*'	6.90ˇ'	7.98'	8.31ˇ*'	7.04ˇ*'
Total polyunsaturated fatty acids	43.74ˇ*'	41.06ˇ*'	47.56'	41.32ˇ*'	42.06ˇ*
Saturated fatty acids/polyunsaturated fatty acids	0.47	0.59ˇ*'	0.40'	0.60ˇ*	0.55ˇ*
n-3/n-6	3.07ˇ*'	3.09ˇ*'	3.62'	2.98ˇ*'	3.02ˇ*'
20:4n-6/18:2n-6	6.84ˇ*'	5.69	5.72'	4.42ˇ*	4.91ˇ*

lipid composition only in cultured mussels: a rise in SFA and 22 NMIFA concentrations and a significant decrease in the n-3 PUFA family (Table 2), which is known to promote increased viscosity of the lipid bilayer and resistance to oxidative stress. The lack of changes in the dominant membrane lipids and fatty acids composition of intertidal mussels under 35 ppt salinity possibly points to their acclimation to the experimental conditions.

When salinity was increased to 45 ppt littoral mussels responded by decreasing cholesterol and 20 NMIFA and SFA content, whereas the concentration of n-3 and n-6 PUFA rose. These modifications presumably led to a decrease in bilayer viscosity and high permeability of mussel gill membranes under hyperosmotic stress. In cultured mussels, on the contrary, simultaneous decrease of n-3 polyenes, arachidonic 20:4n-6 acid and 22 NMIFA were observed. This suggests that the main membrane lipid and fatty acid compensatory response of the mussels to the effect of high ambient salinity depends on their initial habitat (frequent fluctuations in the intertidal zone or stability in the aquaculture).

In addition to the membrane dominant phospholipids, changes in salinity caused modifications in the amount of minor lipid components such as sphingomyelin (SPH), PS and phosphatidylinositol (PI) in the gills of intertidal and cultured blue mussels. An essential structural phospholipid in membranes (alongside with PC and PE), SPH content rises in the gills of both littoral and cultured mussels more significantly in response to seawater desalination (to 15 and 5 ppt) (Tables 1 and

https://doi.org/10.1017/S0032247412000629 Published online by Cambridge University Press

2). Furthermore, SPH is not only a structural component of cell membranes, but also a regulator of cholesterol synthesis (Scheek and others 1997), and quite a number of SPH biosynthesis metabolites participate as secondary messengers in many cellular processes, as well as during exposure to external stress factors (Vance and Vance 2002). Thus, the increased concentration of SPH in the gills of intertidal and cultured mussels suggests this phospholipid contributes to the acclimatisation of the mussels to desalination of seawater.

Phosphatidylserine (PS) content is crucial for cell-volume regulation during the adaptation of bivalves to various ambient salinities. Along with organic molecules, key osmolytic agents in osmoconformers are inorganic ions, namely K^+, Na^+ and Cl^- (Berger 1986; Shakhmatova and others 2006). Studies have shown that in addition to passive ion transport, the cell volume of marine bivalves is regulated by ouabain-sensitive Na^+/K^+-ATPase and ouabain-insensitive Mg^{2+}/Na^+-ATPase (Borgatti and others 2003; Pagliarani and others 2006). The permeability of the cell membrane to ions, and the activity of classical Na^+/K^+-ATPase, integrated into the cell membrane, are largely dependent on the structural organisation of the lipid bilayer, especially the presence of PS in the membrane (Boldyrev 1998). Cultured mussels raised PS content in their gills in response to all studied salinities, whereas in littoral mussels the rise was observed only at salinities of 15 and 45 ppt (Tables 1 and 2). The rise in PS content in the gills of White Sea mussels exposed to various seawater salinities may lead to a modification in the activity of enzymes, ion channels and pumps, as well as membrane-bound osmo- and sodium receptors of gills and mantle tissue, responsible for cell-volume regulation (Berger 1986). However, the activity of these protein components depends not only on the PS content in the membrane, but also on other structural characteristics of the lipid bilayer such as the cholesterol concentration and phospholipid composition (Vance and Vance 2002).

Noteworthy is the rise in phosphatidylinositol (PI) concentration in the gills of littoral and cultured mussels under exposure to all experimental salinities (Tables 1 and 2). Phosphatidylinositol is known to be a key minor component of cell membranes, which plays an important role in essential metabolic processes. It is the precursor for diacylglycerols (DAG) and phosphates such as IP3, which act as signal molecules in animal cells. They regulate the activity of protein kinases A, B and C, which controls many cell functions, such as differentiation, proliferation, metabolism and apoptosis (Vance and Vance 2002; Di Paolo and De Camilli 2006). Furthermore, PI is the main source of arachidonic 20:4n-6 acid, which is the metabolic precursor for the synthesis of eicosanoids, biologically active molecules (Vance and Vance 2002). Modifications in arachidonic acid concentration observed in acclimated White Sea mussels from both habitats (Tables 1 and 2) can be presumed to indicate the activation of the eicosanoid synthesis in gills when ambient salinity changes. Some authors have demonstrated intensified synthesis of prostaglandins, a type of eicosanoids, in bivalves during their acclimation to various seawater salinities (Freas and Grollman 1980).

The present study found that the action of various seawater salinities on intertidal and cultured mussels results in alterations in the amount of membrane lipid components, which are known to influence the phase state of biological membranes. Fluctuations of the lipid bilayer microviscosity are sufficient for activation and development of regulatory reactions which consequently lead to acclimation of the organism (Los and Murata 2004). Biological membranes comprise quite a number of proteins and receptors the activity of which largely depends on the phase state of cell membranes. Permeability of the lipid bilayer to ions, as well as the activity of ion channels and pumps (such as, Na^+/K^+-ATPase or Mg^{2+}/Na^+-ATPase) are predetermined by membrane microviscosity (Hochachka and Somero 1984; Vance and Vance 2002), while fluctuations in the composition of membrane lipids play an essential role in the processes of the mussels' acclimation to various ambient salinities. It was shown, for instance, that when ambient salinity changes, modifications in cholesterol content in membranes of *Mytilus edulis* mussels correlate with the activity of intracellular Ca^{2+}-dependent proteinases (calpains), which perform important functions in cell metabolism, including cell volume regulation (Kyaivaryainen and others 2005; Bondareva and others 2006).

Modifications at the level of membrane lipids in mussel gills in response to a change in seawater salinity facilitate the establishment of optimal fluidity of biological membranes to secure normal functioning of membrane-bound proteins and receptors, as well as cell metabolism in general. Fluctuations in the composition of phospholipid fractions, cholesterol and the range of total lipid fatty acids in response to critical salinity (5 ppt) have similar features, whereas when water salinities were close to physiological values, the modifications in membrane lipids depended on the mussels' initial habitat (intertidal zone or aquaculture).

Acknowledgements

The authors are grateful to staff of the Kartesh White Sea Biological Research Station of the Russian Academy of Science Zoological Institute for permission to carry out research at the station. The study was supported by a grant from the Russian Foundation for Basic Research (08-04-01140-a) and Russian Federation Presidential Programme 'Leading Scientific Schools' (SS-1642.2012.4).

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