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Temperature stress and its impact on bivalve mortality: A review of physiological responses

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Received: March 2024 Accepted: May 2024

Abstract

Temperature significantly influences the distribution and survival of bivalve populations, with elevated temperatures resulting in increased mortality rates. Research indicates that temperature fluctuations can markedly affect bivalve immune responses, including gene expression, hemocyte concentrations, and overall immunocompetence. Higher temperatures impair immune functions, leading to decreased phagocytic activity, compromised immune parameters, and disrupted metabolic processes, which collectively contribute to increased mortality. Understanding the relationship between temperature stress and bivalve survival is crucial for effective population management and for developing strategies to mitigate the negative impacts on bivalve populations in changing ecosystems.

Keywords: Thermal tolerance, Immune Response, Bivalve, Growth

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Introduction

Global warming is causing the Earth's atmosphere to warm up, which, in turn, is leading to an increase in ocean temperatures. According to the Intergovernmental Panel on Climate Change (IPCC), the average global ocean temperature is projected to rise by 0.2°C to 0.5°C by the end of the 21st century under a low-emissions scenario, and by 1.8°C to 4.4°C under a high-emissions scenario (Masanja *et al*., 2023). In coastal areas, rising temperatures can lead to increased seawater evaporation and reduced rainfall, resulting in higher salinity levels. Conversely, these conditions may also cause heavy tropical rainfall, which can lower salinity (Rato *et al*., 2022). Temperature and salinity are key physical factors influencing the abundance and distribution of intertidal organisms like bivalves. Temperature significantly influences bivalve physiology, affecting energy balance, activity, growth, reproduction, feeding, behavior, and respiration. Higher temperatures can enhance seawater evaporation, alter salinity levels, and promote the proliferation of pathogenic microorganisms, which may compromise bivalve immune and metabolic systems, potentially resulting in increased mortality (Xu *et al*., 2016; Kong *et al*., 2023).

The aquaculture industry is playing an increasingly vital role in global food supplies; however, it faces challenges from climate change, globalization, ecological constraints, and shifts in human population dynamics (Harrison *et al*., 2022). In the past decade, extreme weather events associated with global climate change, such as summer heat waves and winter cold spells, have become more frequent. These conditions pose a significant threat to the survival of marine organisms, especially in coastal regions where many species are thought to exist at or near their upper limits of stress tolerance (Carneiro *et al*., 2020).

Bivalves are vital to marine ecosystems, serving as a primary food source for numerous species and playing a significant role in aquaculture. Therefore, understanding their responses to environmental stressors is essential (Alma *et al*., 2023; Masanja *et al*., 2024). Bivalves do not possess effective mechanisms for regulating their body temperature (Mackenzie *et al*., 2014). Under stressful conditions, such as significant fluctuations in temperature and salinity, bivalves typically close their valves to protect themselves from osmotic stress. They also reduce feeding activity and exhibit slower growth and respiration rates, which ultimately leads to alterations in oxygen consumption (Rato *et al.*, 2022). This review highlight the importance of understanding the physiological effects of temperature fluctuations on bivalve populations, which is essential for developing effective management and conservation strategies aimed at enhancing their resilience in challenging marine environments.

Effect of temperature on bivalve growth

Understanding the environmental factors influencing bivalve growth is crucial for effective population management and anticipating future changes (Lamine *et al.*, 2023). Temperature significantly influences bivalve growth by affecting their energy balance and activity levels. Generally, higher temperatures lead to increased growth rates, provided they remain within certain tolerance ranges. Cooler temperatures can inhibit growth and development, leading to lower survival rates and decreased population densities (Yu et al., 2022). Temperature and food availability are well-established predictors of growth rates within species, typically exhibiting positive relationships (Atchadé and Nougbodé, 2024). However, extreme temperatures can negatively impact the growth of bivalves (Rato *et al*., 2022). The optimal temperature range for the survival and growth of bivalves typically 17-24°C, with ideal growth for species such as oysters, clams, scallops, and mussels occurs at an average temperature of 18°C, within a broader range of 12°C to 24°C. However, studies indicate a significant error in this average, with a standard deviation of 2°C (Acquafredda *et al*., 2019). Temperatures exceeding 32°C can cause acute increases in hemocyte levels and gonadal reabsorption in certain species. Furthermore, climate-induced warming and reduced salinity can promote the emergence and spread of pathogenic microorganisms, which negatively impact the immune and metabolic systems of bivalves, leading to significant mortality rates (Zgouridou *et al*., 2022). Research indicates that some bivalve species may experience stress at temperatures above 25°C or below 10°C, with specific thresholds varying by species and environmental conditions (Rahman *et al.*, 2019). Understanding the environmental factors that influence bivalve growth is essential for effective population management and for anticipating the impacts of climate change. While moderate increases in temperature can enhance growth rates, extreme temperatures present significant risks, potentially inhibiting growth and increasing mortality. The relationship between temperature and food availability further complicates growth dynamics. This information is vital for developing strategies to mitigate adverse effects on bivalve populations and to ensure their sustainability in evolving ecosystems.

Effect of temperature on bivalve survival

Bivalve survival is closely linked to their adaptability to temperature fluctuations. Increased temperatures can elevate mortality rates due to heightened metabolic demands and environmental stress. Conversely, bivalves from colder regions may experience decreased survival in warmer conditions, as elevated temperatures place additional strain on their physiological processes. This highlights the critical role of temperature in shaping the distribution and survival of bivalve populations (Saulsbury *et al*., 2019). For example, high temperatures (over 24°C) can lead to increased mortality in species such as the New Zealand Greenshell mussel (*Perna canaliculus*). In this study, Mussels infected with *Photobacterium swingsii* exhibited higher mortality rates at 20°C and 24°C, suggesting that elevated temperatures compromise their immune systems (Azizan *et al*., 2024). The European clam (*Ruditapes decussatus*) also exhibits higher mortality rates in response to sudden temperature fluctuations. The study found that a temperature of 15°C resulted in no mortality, while higher temperatures were associated with increased mortality rates. Juveniles were more susceptible to rising temperatures, leading to increased and quicker mortality rates (Rato *et al*., 2022). In another study, Juvenile oysters (*Crassostrea virginica*) exhibited decreased survival rates at higher temperatures (31°C) in comparison to cooler conditions (24°C) (Stevens and Gobler, 2018). Elevated seawater temperatures significantly affect the survival rates of bivalve larvae, particularly in giant clams such as *Tridacna gigas*. At 33 °C, larval survival was significantly reduced at both 12 and 24 hours post-fertilization compared to lower temperatures of 28°C and 30°C (Enricuso *et al*., 2019). However, the impact of temperature on bivalve mortality significantly varies depending on the species. For example, the larvae of *Mercenaria mercenaria* and *Argopecten irradians* exhibited significant declines in survival at 28°C compared to the optimal temperature of 24°C (Talmage and Gobler, 2011). The survival of bivalve populations depends on their ability to adapt to temperature changes. Elevated temperatures significantly increase mortality rates due to heightened metabolic demands and physiological stress, particularly affecting species from colder environments, which may experience disruptions in their immune systems and a decline in overall health. Furthermore, the vulnerability of juvenile bivalves to temperature fluctuations highlights the importance of considering different life stages when assessing population resilience. Overall, this evidence underscores the critical impact of temperature on bivalve distribution and survival, emphasizing the need for continued research to understand these dynamics in the context of climate change and environmental variability.

Effect of temperature on bivalve immune response

Mollusk immune systems depend on hemocytes to perform various defense functions, including inflammation, wound repair, respiratory burst, phagocytosis, and encapsulation. They also utilize antimicrobial compounds such as alkaline phosphatase (ALP) and acid phosphatase (ACP) to degrade foreign materials (Liu *et al*., 2004; Mackenzie *et al*., 2014). Sub-lethal temperatures can influence bivalve immune systems by affecting metabolism, hemocytes, oxidative stress, and gene expression (Chen *et al*., 2019). A previous study has demonstrated that heat stress can impact the immune response of bivalves, including the Pacific oyster (*Crassostrea gigas*), Mediterranean mussel (*Mytilus galloprovincialis*), and mud cockle (*Katelysia rhytiphora*) (Rahman *et al.*, 2019). Sub-lethal temperatures can significantly impact the immune systems of bivalves by downregulating immune-related genes and altering metabolic processes. Increased temperatures can downregulate stress and immune response genes, such as krs and mydd88 (Almeida *et al*., 2020). High temperatures and *Vibrio* infections in clams (*Meretrix petechialis*) lead to increased apoptosis and oxidative stress, resulting in higher mortality rates compared to those observed at lower temperatures. LPS (lipopolysaccharide) stimulation can activate immune responses in scallops, though its effectiveness diminishes at higher temperatures (Yue *et al*., 2024). In addition, increased temperatures can affect immune functions, reducing phagocytic activity in species such as *Crassostrea gallina* and *C. virginica* at elevated temperatures of 30°C (Matozzo and Marin, 2011). The immune parameters of the green-lipped mussel (*Perna viridis*), including lysozyme levels, esterase activity, phagocytosis, and reactive oxygen species (ROS), significantly decreased following exposure to high temperatures. Similar results were observed in the thick shell mussel (*Mytilus coruscus*) when exposed to high temperatures (Wu *et al*., 2016). Therefore, temperature stress can impair the mussel's ability to respond to pathogens and other threats (Wang *et al*., 2011). Immunological responses to heat exposure are highly dependent on the duration of the exposure and species of bivalves. For example, elevated temperatures, when combined with *Vibrio* infection in clams (*M. petechialis*), triggered a more robust antibacterial immune response. This was evidenced by the increased expression of immune-related genes, including complement C1q-like protein, C-type lectin, big defensin, and lysozyme in the group infected with *Vibrio* at high temperatures (Tian *et al*., 2024). Li *et al.* (2010) observed similar results, finding that the expression levels of immune-related genes in *M. galloprovincialis* varied significantly by season, with defensin, myticin B, and lysozyme genes exhibiting higher expression during the spring and summer months. In another study, heat stress can increase the total hemocyte count (THC) in the hemolymph of bivalves (Hong *et al*., 2021). Liu *et al*. (2004) reported that At 19°C and 22°C, *C. farreri* haemocyte concentrations were significantly lower than at 25°C and 28°C. Conversely, the study showed that temperature significantly affects the immunocompetence of blue mussels (*Mytilus edulis*), particularly influencing hemocyte viability and phagocytic activity. Hemocytes displayed greater viability and phagocytic capacity at lower temperatures (5°C) compared to higher temperatures (10°C and 20°C) (Beaudry *et al*., 2016). Moreover, Mackenzie *et al*. (2014) reported that warming resulted in a reduction of circulating haemocytes in *M. edulis*. Similar results were observed by Trigg *et al*. (2020). They found that immune response-related proteins were less abundant in oysters raised at 29°C compared to those raised at 23°C. Bivalve immune responses are closely linked to environmental temperature, with higher temperatures impairing hemocyte functionality, phagocytic activity, and immune gene expression. As climate change modifies ocean temperatures, these physiological effects may compromise bivalves' ability to combat pathogens, potentially leading to increased mortality rates and changes in population dynamics. Understanding these impacts is crucial for the management and conservation of bivalve species in changing marine ecosystems.

Conclusion

Understanding the environmental factors that influence bivalve growth is crucial for effective population management and for anticipating the impacts of climate change. While moderate increases in temperature can enhance growth rates, extreme temperatures present significant risks, potentially inhibiting growth and increasing mortality. The relationship between temperature and food availability further complicates growth dynamics. As climate change modifies marine environments through temperature fluctuations and changes in salinity, the potential for increased stress and the emergence of pathogens underscores the need for ongoing research. This knowledge is essential for developing strategies to mitigate adverse effects on bivalve populations and to ensure their sustainability in changing ecosystems. Future research will investigate how temperature stress affects bivalve reproduction and gonadal health, considering the functionality of the immune system. This approach aims to provide a comprehensive understanding of the overall impact of temperature on bivalve physiology and survival.

References

Acquafredda, M.P., Munroe, D.M., Calvo, L.M.R. and De Luca, M., 2019. The effect of rearing temperature on the survival and growth of early juvenile Atlantic surfclams (*Spisula solidissima*). *Aquaculture Reports*, 13, 100176 P. DOI:10.1016/j.aqrep.2018.100176

Alma, L., Fiamengo, C.J., Alin, S.R., Jackson, M., Hiromoto, K. and Padilla-Gamiño, J.L., 2023. Physiological responses of scallops and mussels to environmental variability: Implications for future shellfish aquaculture. *Marine Pollution Bulletin*, 194, p.115356. DOI:10.1016/j.marpolbul.2023.115356

Almeida, Â., Solé, M., Soares, A.M. and Freitas, R., 2020. Anti-inflammatory drugs in the marine environment: Bioconcentration, metabolism and sub-lethal effects in marine bivalves. *Environmental Pollution*, 263, 114442 P. DOI:10.1016/j.envpol.2020.114442.

Atchadé, M.N. and Nougbodé, H., 2024. Statistical investigation on the relationship between climate change, food availability, agricultural productivity, and economic expansion. *Heliyon*, 10(**12**), 32520 P. DOI:10.1016/j.heliyon.2024.e32520

Azizan, A., Venter, L., Zhang, J., Young, T., Ericson, J.A., Delorme, N.J., Ragg, N.L. and Alfaro, A.C., 2024. Interactive effects of elevated temperature and *Photobacterium swingsii* infection on the survival and immune response of marine mussels (*Perna canaliculus*): A summer mortality scenario. *Marine Environmental Research*, 196, 106392 P. DOI:10.1016/j.marenvres.2024.106392

Beaudry, A., Fortier, M., Masson, S., Auffret, M., Brousseau, P. and Fournier, M., 2016. Effect of temperature on immunocompetence of the blue mussel (*Mytilus edulis*). *Journal of xenobiotics*, 6(**1**), 5889P. DOI:10.4081/xeno.2016.5889

Carneiro, A.P., Soares, C.H.L., Manso, P.R.J. and Pagliosa, P.R., 2020. Impact of marine heat waves and cold spell events on the bivalve *Anomalocardia flexuosa*: a seasonal comparison. *Marine Environmental Research*, 156, 104898 P. DOI:10.1016/j.marenvres.2020.104898

Chen, Z., Zhang, D., Xing, J. and Zhan, W., 2019. Effects of temperature on haemocyte and granulocyte counts and expressions of immunity-related genes in haemocytes of Scallop *Chlamys farreri* after *Vibrio anguillarum* infection. *Journal of Ocean University of China*, 18, pp. 1163-1173. DOI:10.1007/s11802-019-4180-3

Enricuso, O.B., Conaco, C., Sayco, S.L.G., Neo, M.L. and Cabaitan, P.C., 2019. Elevated seawater temperatures affect embryonic and larval development in the giant clam *Tridacna gigas* (*Cardiidae: Tridacninae*). *Journal of Molluscan Studies*, 85(**1**), pp. 66-72. DOI:10.1093/mollus/eyy051

Harrison, J., Nelson, K., Morcrette, H., Morcrette, C., Preston, J., Helmer, L., Titball, R.W., Butler, C.S. and Wagley, S., 2022. The increased prevalence of Vibrio species and the first reporting of *Vibrio jasicida* and *Vibrio rotiferianus* at UK shellfish sites. *Water research*, 211, 117942P. DOI: 10.1016/j.watres.2021.117942

Hong, H.K., Kim, C.W., Kim, J.H., Kajino, N. and Choi, K.S., 2021. Effect of extreme heatwaves on the mortality and cellular immune responses of Purplish bifurcate mussel *Mytilisepta virgata* (Wiegmann, 1837) (=*Septifer virgatus*) in Indoor mesocosm experiments. *Frontiers in Marine Science*, 8, 794168 P. DOI:10.3389/fmars.2021.794168

Kong, N., Zhao, J., Zhao, B., Liu, J., Li, F., Wang, L. and Song, L., 2023. Effects of high temperature stress on the intestinal histology and microbiota in Yesso scallop *Patinopecten yessoensis*. *Marine Environmental Research*, 185, 105881P. DOI: 10.1016/j.marenvres.2023.105881

Lamine, I., Chahouri, A., Moukrim, A. and Alla, A.A., 2023. The impact of climate change and pollution on trematode-bivalve dynamics. *Marine Environmental Research*, 106130 P.

DOI:10.1016/j.marenvres.2023.106130

Li, H., Venier, P., Prado-Alvárez, M., Gestal, C., Toubiana, M., Quartesan, R., Borghesan, F., Novoa, B., Figueras, A. and Roch, P., 2010. Expression of *Mytilus* immune genes in response to experimental challenges varied according to the site of collection. *Fish & Shellfish Immunology*, 28(**4**), pp.640-648. DOI: 10.1016/j.fsi.2009.12.022

Liu, S., Jiang, X., Hu, X., Gong, J., Hwang, H. and Mai, K., 2004. Effects of temperature on non-specific immune parameters in two scallop species: *Argopecten irradians* (Lamarck 1819) and *Chlamys farreri* (Jones & Preston 1904). *Aquaculture Research*, 35(**7**), pp. 678-682. DOI:10.1111/j.1365-2109.2004.01065.x

Mackenzie, C.L., Lynch, S.A., Culloty, S.C. and Malham, S.K., 2014. Future oceanic warming and acidification alter immune response and disease status in a commercial shellfish species, *Mytilus edulis* L. *PLoS One*, 9(**6**), e99712P. DOI: 10.1371/journal.pone.0099712

Masanja, F., Yang, K., Xu, Y., He, G., Liu, X., Xu, X., Xiaoyan, J., Xin, L., Mkuye, R., Deng, Y. and Zhao, L., 2023. Impacts of marine heat extremes on bivalves. *Frontiers in Marine Science*, 10, 1159261 P.

Masanja, F., Luo, X., Jiang, X., Xu, Y., Mkuye, R. and Zhao, L., 2024. Environmental and social framework to protect marine bivalves under extreme weather events. *Science of The Total Environment*, 174471 P. DOI: 10.1016/j.scitotenv.2024.174471

Matozzo, V. and Marin, M.G., 2011. Bivalve immune responses and climate changes: is there a relationship? *Invertebrate Survival Journal*, 8(**1**), pp.70-77.

Rahman, M.A., Henderson, S., Miller-Ezzy, P., Li, X.X. and Qin, J.G., 2019. Immune response to temperature stress in three bivalve species: Pacific oyster *Crassostrea gigas*, Mediterranean mussel *Mytilus galloprovincialis* and mud cockle *Katelysia rhytiphora*. *Fish & Shellfish Immunology*, 86, pp. 868-874. DOI:10.1016/j.fsi.2018.12.017

Rato, A., Joaquim, S., Matias, A.M., Roque, C., Marques, A. and Matias, D., 2022. The impact of climate change on bivalve farming: combined effect of temperature and salinity on survival and feeding behavior of clams *Ruditapes decussatus*. *Frontiers in Marine Science*, 9, 932310P. DOI: 10.1016/j.fsi.2018.12.017

Saulsbury, J., Moss, D.K., Ivany, L.C., Kowalewski, M., Lindberg, D.R., Gillooly, J.F., Heim, N.A., McClain, C.R., Payne, J.L., Roopnarine, P.D. and Schöne, B.R., 2019. Evaluating the influences of temperature, primary production, and evolutionary history on bivalve growth rates. *Paleobiology*, 45(**3**), pp. 405-420. DOI:10.1017/pab.2019.20

Stevens, A.M. and Gobler, C.J., 2018. Interactive effects of acidification, hypoxia, and thermal stress on growth, respiration, and survival of four North Atlantic bivalves. *Marine*

Ecology Progress Series, 604, pp. 143-161. DOI:10.3354/meps12725

Talmage, S.C. and Gobler, C.J., 2011. Effects of elevated temperature and carbon dioxide on the growth and survival of larvae and juveniles of three species of northwest Atlantic bivalves. *PloS One*, 6(**10**), e26941 P. DOI:10.1371/journal.pone.0026941.

Tian, J., Wang, D., Wang, H., Huan, P. and Liu, B., 2024. The combination of high temperature and Vibrio infection worsens summer mortality in the clam *Meretrix petechialis* by increasing apoptosis and oxidative stress. *Fish & Shellfish Immunology*, 149, 109542P. DOI: 10.1371/journal.pone.0026941

Trigg, S.A., Mitchell, K.R., Thompson, R.E., Eudeline, B., Vadopalas, B., Timmins-Schiffman, E.B. and Roberts, S.B., 2020. Temporal proteomic profiling reveals insight into critical developmental processes and temperature-influenced physiological response differences in a bivalve mollusc. *BMC Genomics*, 21, pp. 1-15. DOI:10.1186/s12864-020-07127-3

Wang, Y., Hu, M., Shin, P.K. and Cheung, S.G., 2011. Immune responses to combined effect of hypoxia and high temperature in the green-lipped mussel *Perna viridis*. *Marine pollution Bulletin*, 63(**5-12**), pp. 201-208. DOI:10.21072/mbj.2022.07.3.01

Wu, F., Lu, W., Shang, Y., Kong, H., Li, L., Sui, Y., Hu, M. and Wang, Y., 2016. Combined effects of seawater acidification and high temperature on hemocyte parameters in the thick shell mussel *Mytilus coruscus*. *Fish & Shellfish Immunology*, 56, pp. 554-562. DOI:10.1016/j.fsi.2016.08.012

Xu, X., Yang, F., Zhao, L. and Yan, X., 2016. Seawater acidification affects the physiological energetics and spawning capacity of the Manila clam *Ruditapes philippinarum* during gonadal maturation. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 196, pp. 20-29. DOI:10.1016/j.cbpa.2016.02.014

Yu, J., Yin, Z., Zhang, Y., Bi, J., Yan, X. and Nie, H., 2022. Effects of high water temperature on physiology, survival, and resistance to high temperature air-exposure in the Manila clam *Ruditapes philippinarum. Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology*, 262, 109469 P. DOI:10.1016/j.cbpc.2022.109469

Yue, C., Zhang, K., Liu, Z., Lü, W., Guo, H., Zhao, L., Song, X. and Fang, J.K.H., 2024. The role of the TLR4-MyD88 signaling pathway in the immune response of the selected scallop strain “Hongmo No. 1” to heat stress. *Animals*, 14(**3**), pp.497. DOI:10.3390/ani14030497

Zgouridou, A., Tripidaki, E., Giantsis, I.A., Theodorou, J.A., Kalaitzidou, M., Raitsos, D.E., Lattos, A., Mavropoulou, A.M., Sofianos, S., Karagiannis, D. and Chaligiannis, I., 2022. The current situation and potential effects of climate change on the microbial load of marine bivalves of the Greek coastlines: An integrative review. *Environmental Microbiology*, 24(**3**), pp. 1012-1034. DOI:10.1111/1462-2920.1576