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Destruction of the Kakhovka Dam (Ukraine) and Its Impact on Mediterranean Mussel (*Mytilus galloprovincialis*) Populations in the Gulf of Odesa

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Abstract: Following the deliberate destruction of the Kakhovka Dam (Ukraine; 6th June, 2023), freshwater from the reservoir flowed into the Black Sea, resulting in widespread desalination (< 8‰) and pollution near the Odessa coast, negatively affecting populations of Mediterranean mussel *Mytilus galloprovincialis*. Subsequent surveys revealed mass mortalities on both natural (rock) and artificial (traverses, piers) substrates at depths of 1–3 m. Maximal valve length of dead mussels was 61 mm on both natural and artificial substrates, with average length of dead mussels on rock increasing with depth from 41.33±1.37 mm at 1 m to 45.69±3.06 mm at 3 m. In all cases, linear dimensions of dead mussels exceeded 40 mm, suggesting that critically low salinity wiped out the most valuable reproductive cohort of the population in the affected region.

Key words: bivalves, Black Sea, desalination impacts, technogenic disaster, Kakhovka Reservoir, mussel mortality

Introduction

The deliberate destruction of the Kakhovka Dam, which took place on 6th June, 2023, led to the worst environmental disaster on the territory of Ukraine resulting from the Russian invasion to date (Afanasyev 2023, Minicheva et al. 2023, Tuchkovenko et al. 2023). As a result of the destruction of the dam, residential buildings, petrol stations, landfill sites, sewage systems, cattle burial grounds, cemeteries and burial sites were flooded (Chernogor et al. 2024), with the result that raw sewage, industrial wastewater, agricultural fertilisers and pesticides, animal carcasses and oil and hydrocarbons were washed from the flooded areas, entering the north-western part of the Black Sea (Jiang et al. 2025). The destruction of the Kakhovka Power Plant and the flooding of retail petrol stations alone led to the release of ca. 450 tonnes of petroleum products into the floodwaters (Chernogor et al. 2024, Shumilova et al. 2025). Furthermore, a high pollutant load had accumulated in the reservoir sediments prior to the disaster and, following the dam collapse, ca. 0.78×10^{-3} km^3 of contaminated sediment was washed from the reservoir (Shumilova et al. 2025). Not long after the explosion, bacteriological and chemical pollutants were recorded in the lower Dnipro River, the Dnieper-Bug Estuary and the north-western part of the Black Sea (Gleick et al. 2023, Vyshnevskyi et al. 2023). The river plume finally reached the Danube delta on 17th June 2023, having affected ca. 7,300 km^2 (Vyshnevskyi et al. 2023, Shumilova et al. 2025). In addition to the aforementioned pollutants, however, freshwater from the reservoir reached the coastal shelf of the north-western Black Sea around two days

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after the explosion; this may have caused even more severe and, potentially, longer-lasting damage (Minicheva et al. 2023) by causing significant changes in Black Sea flora and fauna, and the mass mortality of coastal biota (Minicheva et al. 2023, Kvach et al. 2025). This event is now considered the worst man-made disaster to hit the region in recent decades and it is predicted that the environmental consequences will remain observable for ten years or more. The damage to many ecosystems is likely to be irreparable, prompting calls to declare the action as 'ecocide' (Chernogor et al. 2024).

In addition to being a valuable food source (Gracia 1996, Jahutka et al. 2006), marine bivalves are important ecosystem engineers with the ability to alter ecosystem functions. Mollusc respiration and nutrition rely strongly on filtration (Finenko et al. 1990, Maire et al. 2007), during which small planktonic organisms and suspended organic matter are filtered out of the seawater, cleaning it and enriching it with dissolved organic substances necessary for the development of macrophytes (Govorin et al. 2004, Govorin & Shatsillo 2010). Through this biodeposition they promote vegetative productivity and, thus, play an important role in many other ecosystem processes (Jordan & Valiela 1982, Newell 2004). In addition, mussel settlements on concrete traverses and breakwaters encourage the formation of coastal microbiological features that act as natural biofilters by accumulating allogenic microflora (Govorin 2006, Bone et al. 2022, Hayek et al. 2023). Thus, any change in water quality parameters (e.g. salinity) that negatively impacts bivalve populations could also have significant negative impacts on their ecosystem service contributions (Honig et al. 2015, Catherine et al. 2024), with changes in their population dynamics and/or distribution leading to trophic cascades with wider ecosystem consequences (Jordan & Valiela 1982, Bertness 1984). Typical factors adversely affecting marine mussel assemblages include eutrophication, decreased salinity and prolonged hypoxia of demersal water, all of which can cause mortality in benthic species (Shurova 2000, Shurova & Stadnichenko 2004, 2008, Zaika et al. 2011). Chronic impacts may include a decrease in filtration activity, which can negatively impact growth rates and soft body weight parameters and increase overall mortality rates. Secondary effects may include deterioration in coastal recreational conditions due to an increase in suspended matter and potentially harmful waterborne bacteria (Govorin 1994).

The Mediterranean mussel *Mytilus galloprovincialis* (Lamarck, 1819; Bivalvia: Mytilidae) is a widely distributed marine bivalve with a natural range covering the North-East Atlantic, the Mediterranean and the Black Sea, with introduced populations also found in the Arctic, Indian and Pacific Oceans (Palomares & Pauly 2025). The species forms dense demersal settlements that can have both negative (e.g. through displacement) and positive (e.g. by providing a hard substrate for invertebrates and shelter for fish) impacts on the composition and structure of benthic communities (Çinar & Gonlugur-Demirci 2005, Çinar et al. 2008, Bondarev 2013). Furthermore, it is an important and commercially valuable mariculture species (including Integrated Multi-Trophic Aquaculture, see Peharda et al. 2007, Gvozdenović et al. 2017, Della Malva et al. 2024), with worldwide annual production (fresh and canned) at > 100,000 tonnes (Figueras 2009).

Mediterranean mussel assemblages are common along the north-western Black Sea coastal zones, where they are an important commercial species and typically support a high density and diversity of other aquatic organisms (Teacă et al. 2010, Vorobyova et al. 2017, Varigin 2018). While the mussels usually display high thermo-plasticity (Suprunovich & Makarov 1990, Govorin & Shatsillo 2012, Rosioru 2014), optimal salinity levels for healthy development in the Black Sea are limited to approximately 14–25‰ (Ivanov & Borovinskiy 1986, Kholodov et al. 2010, Shurova 2013), making them highly susceptible to sudden changes in water quality, as seen in the immediate aftermath of the destruction of the Kakhovka Dam. Initial surveys immediately after the disaster recorded salinity levels of < 8‰, i.e. below levels critical for the existence of many species, with mass mortalities of bivalves recorded down to 3 m, including species considered more resistant to such stress factors such as *Mytilaster lineatus* (Gmelin, 1791) (Minicheva et al. 2023, Kvach et al. 2025). Given the ecological, biodiversity and economic value of Black Sea Mediterranean mussel populations, this study follows on from the initial surveys by determining specific impacts on Mediterranean mussels in the Gulf of Odesa (Ukraine) following the introduction of large volumes of desalinated and polluted transitional waters from the Dnieper-Bug Estuary.

Material and Methods

Sampling

Standard sampling of Mediterranean mussels took place over June–July 2023; a period that, coincidentally, included samples before (7th June) and after (29th June, 15th and 28th July) the destruction of the Kakhovka Dam. Investigators with scuba-diving gear obtained mussels using 10×10 cm benthos frames along transects at depths of 1 to 5 m on natural rock surfaces and from the surfaces of concrete traverses at depths of 1 to 2 m near Cape Malyi Fontan, Gulf of Odesa (46°26′23.7′′N; 30°44′29.4′′E; Fig. 1). In each case, mussels were sampled in three replicates at each depth along each transect (Table 1). The mussels were placed in plastic bags and moved to the beach, where they were washed through a system of three sieves with the final sieve having a 1-mm mesh. The material from each sieve was then placed in a jar and preserved in a 4% formaldehyde solution. All samples were then compared with previous samples from the Institute of Marine Biology database (Ukraine National Academy of Sciences) taken from a depth of 2.5-9.5 m between 2001–2020 to evaluate long-term changes in population features.

The average number of mussels and of dead individuals was calculated for each 1 m^2 of substrate surface, after which the average biomass was calculated as the total weight of living mussels per 1 m^2 substrate surface. The length of each mussel was then measured to the nearest 0.1 mm, with valve length calculated according to Cheliadina (2007) and the wet mussel weight was calculated to the nearest 0.001 g. Differences in length-weight relationships between living and dead mussels were identified using the formula , where *a* and *b* were allometric coefficients determined by empirical data.

To determine salinity, sea water samples were taken at the same time as mussel sampling for testing in the laboratory. Analysis of variation in values of sea water salinity was based on comparison with data previously published in Minicheva et al. (2023).

Statistical analysis

The total annual production of mussels was calculated for each mussel population, using an empirical multiple regression equation based on data for mussel biomass and average total individual mass (Stadnichenko & Shurova 2000):

$$\ln P=1.004\times\ln B-0.484\times\ln W(R^2=0.970;SE=0.237),$$

where P is annual production in g/m^2 per year; B is mollusc biomass in a population in g/m^2; W is weight of a specimen in g; R^2 is the coefficient of determination and SE - the standard error.

The biomass of dead mussels was calculated as the total weight of dead individuals per 1 m^2 substrate surface, while the annual survival rate (V, %) was calculated using the formula of Stadnichenko (2010):

$$V = 0.84\times e^{-P/B}$$

The linear relationship between individual length (L) and total weight (W) was estimated through regression analysis, using the formula:

$$\ln W=2.728\times\ln L-8.607(R^2=0.984;r=0.992)$$

The calculations were performed using the Statgraph Plus 5.0 statistical package. All data were first log10-transformed to normalise/homogenise any variance. Any significant variation in individual shell length or total mass was then determined using one-way analysis of variance (ANOVA). All results are presented as means±SE with a significance level of $p < 0.05$.

Fig. 1. Map of the Cape Malyi Fontan sampling area in the Gulf of Odesa, Black Sea, Ukraine.

Table 1. Annual population parameters for Mediterranean mussels collected near Cape Malyi Fontan, Gulf of Odesa. *H* = depth, m; *N* = number, ind/m^2; *B* = biomass, g/m^2; *W* = average individual weight, g; *P* = total annual production, g/m^2; *V* = survival rate, %.

Year	*H*	*N*	*B*	*W*	*P*	*V*
2001	5.0	6250	23593.3	3.78	12905.5	57.8
2007	2.0	6775	11475	1.69	9112.5	44.7
2008	3.4	3825	15850.7	4.14	8283.6	59.3
	7.5	1325	4660	3.52	2621.4	57
2012	6.4	2875	9795.3	3.41	5614.5	56.4
	8.1	2700	12207.8	4.52	6107.1	60.6
	8.6	2650	8106.6	3.06	4891.6	54.7
	9.5	7125	11124.7	1.56	9307.2	43.3
2016	3.0	5400	15399	2.852	9637.7	53.5
	3.0	3600	13742.2	3.817	7465.2	58.1
	3.0	3875	22792.8	5.882	10064.2	64.3
2017	3.0	2325	16558.5	7.122	6656.4	66.9
	3.0	2725	15932.5	5.847	7045.4	64.3
	3.0	1625	10853	6.679	4493	66.1
	3.0	1350	12018.7	8.903	4331.2	69.7
2018	3.0	1350	11103.2	8.225	4156.4	68.8
	3.0	4150	17886.2	4.310	9171.6	59.9
	3.0	4100	14922.7	3.640	8298.3	57.3
	5.0	1967	19042.6	9.68	6602	56.1
2019	3.0	3300	11084	3.359	6400.3	60.9
	3.0	4575	21150	4.623	10490.4	62
	3.0	2950	14656	4.969	7010.1	53.5
2020	2.0	10267	15411.1	1.50	13164.3	42.6
	4.3	3100	14977.9	4.83	7261.9	61.6
	6.1	3567	28849.7	8.09	10931.7	68.5
	8.0	1700	8366.67	4.92	4011.1	61.9
2023	1.0	1267	5091.3	4.018	2687.2	59
	2.0	3133	16849.3	5.378	7760.1	63.1
	3.0	13200	19300	1.460	16705	42.1
	4.0	10100	25724.7	2.547	17040.2	51.6
	5.0	1833	22958.3	12.525	7031.7	73.6
Mean		4032±515	15209.2±1041.8	4.866±0.462	7979.1±636.9	59.2±1.5

Results

Interannual changes in parameters of mussel population before and after the dam discharge

Over the period for which data were available (2001-2023), the mean number of mussels found on natural substrate (rock, stone) varied widely year-by-year: from 1325 ind/m^2 in 2008 to 13200 in 2023 (average 4032 ind/m^2), while the mean biomass over the same period ranged from 4660 g/m^2 in 2008 to 28849.7 in 2020 (average 15209.2 g/m^2; Table 1). Similarly, total annual production varied from 2621.4 g/m^2 per year in 2008 to 17040.2 g/m^2 in 2023 (average 7976.8 g/m^2 per year). Both the lowest and the highest mean individual mussel weight and the mean average survival rate for the study period occurred in 2023, with weight ranging from 1.460 g at a depth of 3 m to 12.525 g at 5 m (average for all years = 4.866 g) and survival from 42.1 at 3 m to 73.6% at 5 m (average for all years =

57.8%; Table 1). The average mussel valve length for all depths (1-9.5 m) showed no significant difference by year, ranging from 13.04 to 37.82 mm over the entire study period. By depth, maximal valve size ranged from 94.2 mm at a depth of 3 m in 2018 to 112.1 mm at 6 m in 2020, both from the same site (Table 1). There was a clear difference in modal mollusc length classes among years, with mussels of 20-50 mm dominant between 2007 and 2019 (Table 1). The maximum number of settled juveniles was registered in the spring of 2006, 2020 and 2023, when juveniles of 10-mm dominated. Prior to the Kakhovka Dam explosion in 2023, the proportion of mussels in the 1–10 mm size class varied between 61.2% and 80.4%.

Mussel mortality

Control observations carried out before the influx of desalinated water following the destruction of the Kakhovka Dam (7th June, 2023) indicated high variation in mussel numbers, ranging from 1267 ind/m^2 at 1 m to 13200 ind/m^2 at 3 m (Table 2) and rock settlement biomass varying from 5091.3 g/m^2 at 1 m to 25724.7 at 5 m (Table 2). Average individual mussel weight also varied with depth, ranging from 1.460 g at 3 m to 12.525 g at 5 m. No empty mussel shells (i.e. dead mussels) occurred in any samples prior to the disaster.

The first mussel mortalities were observed following the Kakhovka Dam explosion, in samples taken at 1–3 m on both natural (rock, stone) and artificial (concrete traverses, piers) substrates on 29th June, 2023 (Table 2). While a single dead individual was recorded at 4 m, which did not exceed measurement error; thus the 4-m mussel population was not considered further when calculating biomass of dead molluscs. This decline in all mussel size cohorts at depths of 1–3 m coincided with a steep drop in local salinity levels to ca. 4‰ during June 2023. Overall, between 7th and 29th June, mussel numbers in rock settlements decreased from 5867±3706 ind/m^2 to 2211±789 and biomass - from 13746.9±4385.2 g/m^2 to 5855.2±1642.5, though some improvement in these figures was observable as early as July 2023, by which time local salinity had increased to 14-15‰ (Fig. 2). Over the same period (7th–29th June), the average weight of living mussels decreased from 3.619±1.149 g to 1.04±0.171 g (Fig. 3).

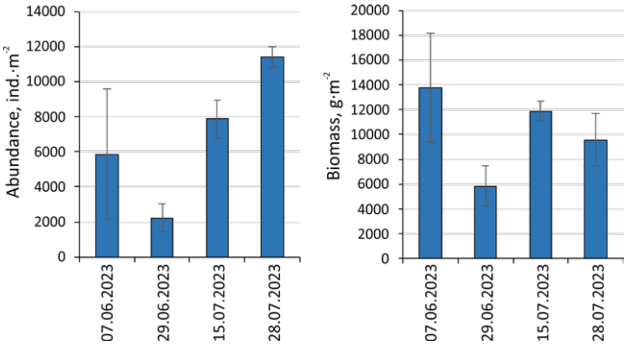


Fig. 2. Changes in numbers and biomass in mussel settlements on natural substrate near Cape Malyi Fontan between June and July 2023.

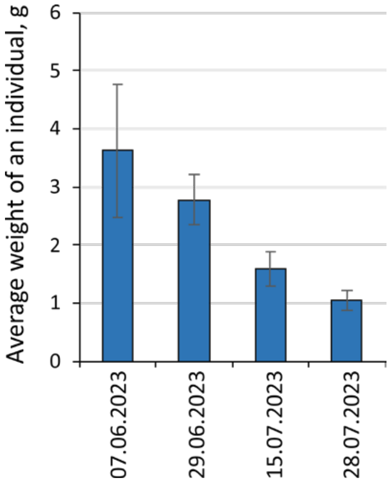


Fig. 3. Changes in average mussel weight on natural substrate near Cape Malyi Fontan between June and July 2023.

The maximal biomass of dead mussels on natural rock substrate was registered on 29th June at a depth of 3 m, with levels at 8015.3 g/m^2 or 57.1% of all molluscs, compared with a live mussel biomass at the same depth of just 6030.7 g/m^2 (Fig. 4). The average weight of dead individuals on rock substrate at 1–3 m was 5.928±0.364 g, varying from 4.974±0.430 g at 1 m to 7.118±0.903 at 3 m. In comparison, the average weight of live individuals at 1-3 m was significantly lower (2.186±0.353 g; Fig. 5). Likewise, on artificial substrate (traverses), while the average weight of all mussels at 1-2 m varied from 6.595 to 10.697 g (mean 7.891±0.842 g), the average weight of living mussels was just 0.387±0.09 g. Following the influx of fresh water, the majority of larger (heavier) mussels had died on both natural and artificial substrates (Fig. 5).

The average mussel length on the rock substrate ranged from 41.33±1.37 mm at a depth of 1 m to 45.69±3.06 mm at 3 m. Almost all dead individuals recorded on 29th June, 2023 were ≥30 mm long; however, from 15th July, 2023 individuals of 20 mm were being registered as dead (Fig. 6). On the traverses, the average length of dead mussels at depths of 1-2 m was slightly greater: 48.53±2.24 mm; however, on both natural and artificial substrates,

Table 2. Number (*N*, ind/m^2), biomass (*B*, g/m^2) and average weight (*W*, g) of living and dead mussels on natural (rock) and artificial (traverses, piers = AS) substrates in the Gulf of Odesa, Black Sea; *H* = depth, m; *P* = total annual production, g/m^2; *V* = survival rate, %.

Date	H	N_{live}	B_{live}	W_{live}	P	V, %	N_{dead}	B_{dead}	W_{dead}	B_{dead} / B_{live}, %
Before Kakhovka Dam destruction										
07.06.2023	1	1267	5091.3	4.018	2687.3	59	0	0	0	0
	2	3133	16849.3	5.378	7760.1	63	0	0	0	0
	3	13200	19300	1.460	16716. 8	42	0	0	0	0
	4	10100	25724.7	2.547	17040.2	52	0	0	0	0
	5	1833	22958.3	12.525	7031.7	74	0	0	0	0
After Kakhovka Dam destruction										
29.06.2023	1	3767	8608.3	2.285	5983.5	50	133	494.47	3.718	5.4
	2	1200	2926.7	2.440	1962.2	51	667	3775.7	5.661	56.3
	3	1667	6030.7	3.618	3351.1	57	1067	8015.3	7.512	57.1
	4	7067	24660.3	3.489	14024.9	57	33	340.3	10.312	1.6
	5	3700	19676.7	5.318	9117.3	63	0	0	0	0
15.07.2023	1	6300	13194	2.094	9583.1	48	933	4144.8	4.442	23.9
	2	9933	10485.3	1.056	10597.7	36	667	4073.3	6.107	27.9
	3	7367	11937.3	1.620	9813.2	44	567	4033.3	7.113	25.6
	4	3900	29090	7.459	11461	67	0	0	0	0
	5	26400	17104	0.648	21939.5	28	0	0	0	0
	AS 1	18667	8847.7	0.474	13168.6	23	433	2858.0	6.600	24.4
	AS 2	15533	4657.7	0.300	8628.1	16	200	2139.4	10.697	31.5
28.07.2023	1	12567	6326	0.899	6897.8	34	0	0	0	0
	2	10733	8834.7	0.840	9968.4	32	0	0	0	0
	3	10933	13569.7	1.381	12057.2	41	0	0	0	0
	4	13867	16558.3	1.682	13384.2	45	0	0	0	0
	5	16133	18952	1.878	14531.1	46	0	0	0	0
	AS 1	9833	9615.3	1.279	8854.6	40	0	0	0	0
	AS 2	11133	7406	0.783	8639.4	31	0	0	0	0

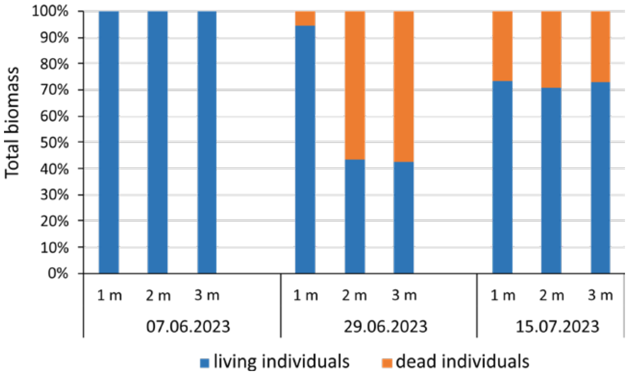


Fig. 4. Ratio of total biomass of living and dead mussels on natural rock substrate by depth.

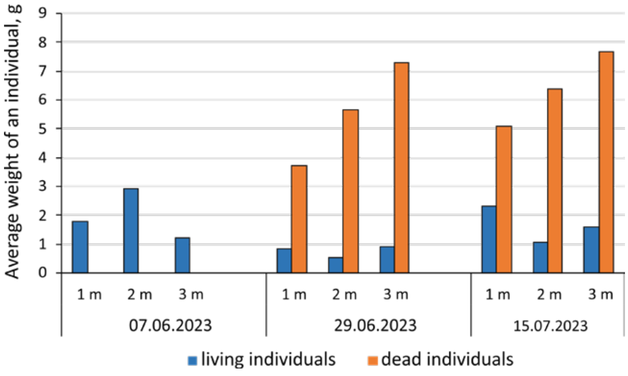
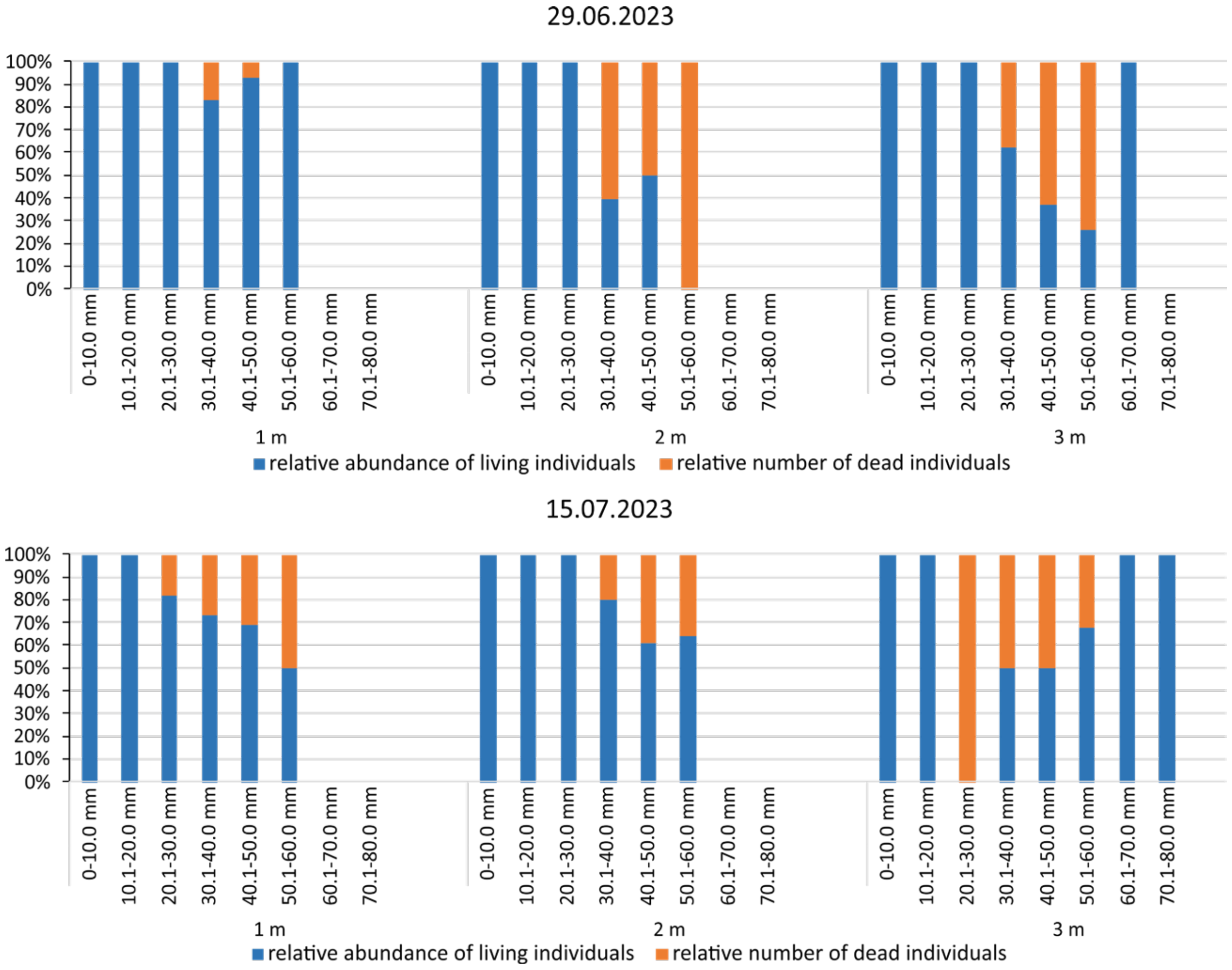


Fig. 5. Ratio of average weight of living and dead mussels on natural rock substrate by depth.


29.06.2023

15.07.2023

Fig. 6. Changes in the ratio of living and dead mussels of different size groups at depths of 1–3 m.

the maximal length was 61 mm. By 28th July, 2023 no further dead mussels were registered on either substrate type, though biomass and average weight remained below levels determined prior to the technogenic disaster (see Figs. 2, 3).

Analysis of variance revealed highly significant differences ($F = 10.17$; $p < 0.001$) between mean annual mussel production before and after exposure to desalinated water. Interestingly, following the relatively long period of critically low salinity, the average annual production of mussels increased to 11281 g/m^2 per year, despite the survival rate dropping significantly to 40.4±1.9% from 59.2±1.5% prior to the disaster ($F = 56.44$; $p < 0.001$).

Discussion

The Kakhovka Dam technogenic disaster has had a significant negative impact on the aquatic fauna of the north-western Black Sea. Approximately two days after the explosion, freshwater from the reservoir reached the seacoast and the most severe, impactful phase of this ecological disaster began, during which there were numerous indications of abnormal abiotic factors impacting on hydrobiont communities (Minicheva et al. 2023). The most pronounced changes in benthic communities occurred at depths up to 3 m, i.e. the coastal zone, with changes in the trophic status of the marine communities contributing to the rapid growth of detritivores and plant-detritus invertebrates, with knock-on negative effects on the region's aquatic maricultural resources. Not only were significant numbers of commercial freshwater fish species released into the marine ecosystem, most of which died in the weeks following the tragedy (Minicheva et al. 2023, Kvach et al. 2025), but prolonged exposure to critically low salinity levels led to mass mortalities in Mediterranean mussel settlements at depths up to 3 m, resulting in a significant decrease in average mussel size and total biomass and a reduction in the mean survival rate. At peak reduced salinity, most mussels with length of 40 mm and above had died, i.e., the most valuable reproductive cohorts of the region's Mediterranean mussel population. This has important implications as mussel fertility is known to be dependent on the population's size structure. For example, in the Black Sea ecosystem, Pirkova et al. (1999) recorded mussel fertility in the Crimea region at 0.15 million eggs for shell lengths of 25 mm to 1.9 million eggs for 55 mm, while Shurova & Zolotarev (2003) recorded 0.046 million eggs for shell lengths of 25 mm and 2.60 million eggs for 55 mm in natural settlements in the Gulf of Odesa. Thus, loss of the majority of mussels with shell lengths of > 40 mm has contributed not only to a significant commercial loss but also to a significant decrease in the future reproductive potential of mussel populations.

Mussels, as sedentary filter feeders, are highly sensitive to changes in temperature, salinity and/or nutrient availability (Westerbom et al. 2002, Riisgård et al. 2003, Hamer et al. 2008, Keskin et al. 2020), any of which can result in large-scale population reductions, which in turn can significantly impact water quality and ecosystem functioning, increasing the risk of eutrophication and further mass mortality events. Several previous Mediterranean mussels mass mortalities have been recorded, either due to unusually high temperatures (Tsuchiya 1983, Capelle et al. 2021, Mandić et al. 2024), seawater pollution (Coppola et al. 2017, 2021, Leite et al. 2023, Uguen 2024) or insufficient food supply (Bracchetti et al. 2024), sometimes in combination with parasitic infestations (Acarlı et al. 2020, Charles et al. 2020, Richard et al. 2020). Indeed, environmental stress has been shown to increase mussel susceptibility to disease, which may then trigger a mass mortality (Di Camillo & Cerrano 2015). Overall, however, the highest impacts on mussel activity are generally ascribed to increases in water temperature and declines in water salinity (Hiebenthal et al. 2012, Riisgård et al. 2014, 2015; present study).

The Mediterranean mussel, an Atlanto-Mediterranean marine species, survives in the Black Sea under atypically low saline conditions (Zaika et al. 1990, Shurova 2001, Rosioru 2014, Freitas et al. 2017). While the optimal salinity for larval development in the species is generally up to 15‰, mass mortalities may be observed at levels of 12‰ (Shtyrkina 1986), with juveniles < 20 mm long and larger individuals being particularly susceptible (Shurova 2013). A sharp slowdown in growth has been observed at salinity levels of 8‰ (Ivanov et al. 1989, Kholodov et al. 2010), along with reduced filtration activity, with filtration (i.e. breathing) ceasing completely if salinity is not restored to optimal levels relatively quickly (Shurova 2001). Furthermore, previous surveys have confirmed that changes in seawater salinity levels can affect mussel population size structure, growth rate, individual lifespan and population phenotypic structure (Shurova 2001, 2013, Stadnichenko et al. 2013).

In our study, the most damaging impacts on natural mussel settlements were caused by the drop in salinity to around 4-8‰, observed between 8th and 26th June, 2023 at 1-3 m (Minicheva et al. 2023), four days after freshwater from the Kakhovka Dam collapse reached the Gulf of Odesa. During that period, surface water salinity decreased significantly, from 13‰ on 7th June to 7.4‰ on 9th June, reaching a minimum of 3.95‰ on 11th June, 2023. Salinity levels remained at around 4‰ for some time, which was three times lower than the minimum permissible concentration of 12‰, gradually increasing to 15‰ by 26th June following mixing and drift-rush (Minicheva et al. 2023). Such an abrupt and relatively long-term decrease in seawater salinity was directly responsible for the mass mortality of mussels on both natural and artificial substrate types. The average biomass of dead mussels at depths of 1-3 m on natural rocky substrates had reached 4095.2±2177 g/m^2 by the end of June 2023 or 39.6% of total population biomass prior to the disaster. By the end of July 2023, the proportion of dead mussels by biomass at 1-3 m had dropped to 25.8% on natural substrate and to 28% at 1-2 m on artificial substrate, i.e. mortality rates on both substrate types were similar. Overall, the average biomass of dead mussels at 1-3 m (all substrates) was 4089.5±973.7 g/m^2.

Environmental stress in the form of extreme changes and/or fluctuations in temperature and salinity affect both the abundance and adaptability of species, which, in turn, can have knock-on effects on biodiversity at all levels, from genes and genomes to individuals, populations, species, ecosystems and biota as a whole (Hamer et al. 2008). In our study, the increase in average total mussel production on hard substrates, following the disaster, indicates a gradual rejuvenation of the settlement, with the highest production levels more-or-less characteristic of mussel settlements being characterised by a high proportion of juveniles (Shurova & Stadnichenko 2001), i.e. typical for settlements with high mortality rates. In such cases, the rate of organic matter turnover tends to be significantly higher than in settlements with more complex age structures, where survival rates are at their maximum, as also confirmed by the decrease in mussel survival rate in our own study following the disaster. Under the present conditions, therefore, survival and spread of Mediterranean mussels throughout the Black Sea is likely to be restricted for some time.

Conclusion

Our results showed that prolonged exposure of commercially important Mediterranean mussels to critically low salinity (below 8‰) led to i) a mass die-off of the reproductive population cohort and ii) a decrease in average size and total biomass of surviving mussels. Our results highlight the importance of recognising the impact of multiple environmental threats, e.g. pollution and critical declines in salinity, on key commercial marine bivalve species. Only by doing so can we fully understand and mitigate potential impacts on ecosystem resilience and dynamics under changing environmental conditions.

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