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REVIEW

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Biodiversity effects of the Russia–Ukraine War and the Kakhovka Dam destruction: ecological consequences and predictions for marine, estuarine, and freshwater communities in the northern Black Sea

Yuriy Kvach[1†], Carol A. Stepien[2*†], Galyna G. Minicheva[1] and Pavlo Tkachenko[3^]

Abstract

Background The effects of war on biodiversity, habitats, ecosystem services, and water, seafood, and fishing resources are complex and long-lasting, yet their ongoing environmental analyses are limited. The Russia–Ukraine War (2022–present) comprises a unique ecological situation to examine biodiversity effects on the distinctive cold-temperate northern Black Sea ecosystem, which has an intriguing biogeographic history and high endemism resulting from geographic isolation and differentiation.

Results We summarize negative and positive effects from the War on the aquatic (marine, estuarine, and freshwater) biota and their habitats, focusing on investigations by the Institute of Marine Biology, National Academy of Sciences of Ukraine. Negative effects include toxins and habitat damage from oil spills, shelling, mining, explosions, flooding, and fires; along with disregard of Protected Areas. Positive effects are reduced anthropogenic loads from less shipping, fishing, trawling, recreation, hydraulic engineering, construction, and tourism. The Kakhovka Dam's destruction on June 6, 2023 was the greatest ecological catastrophe to date, causing extensive downstream flooding with freshwaters and pollutants that destroyed many populations and habitats. We discern that many effects have been temporary, with habitats and species replenishing, and some reverting to their historical biota characteristic of lower salinity regimes. However, significant habitat destruction, disturbances, and pollutant damages remain. Since many of the native species evolved in conditions favoring broad salinity, temperature, and oxygen tolerances, the northern Black Sea ecosystem appears pre-adapted for ecological recovery and persistence, which may equate to ecological resilience during and after the War.

Conclusions The native biota exhibits long-term adaptiveness to marked salinity and temperature fluctuations, alongside a background of invasive species. An evolutionary and recent history of broad environmental tolerances by a large proportion of Black Sea species may enhance their ability to withstand marked environmental changes,

†Yuriy Kvach and Carol A. Stepien joint first authors and contributed equally to this review paper.

^Pavlo Tkachenko is deceased in 2024, and this area now is occupied by Russian Forces.

*Correspondence:
Carol A. Stepien
Stepien.Carol@gmail.com; StepienCA@si.edu
Full list of author information is available at the end of the article

including habitat destruction, as during the Kakhovka Dam's breakage and other stressors that continue during the Russia–Ukraine War. The Black Sea community's overall ecological resilience is likely to facilitate persistence and adaptation to the War's effects and the accelerating impacts of climate change, increased global transportation, and invasive species—meriting worldwide conservation agency focus and cooperation.

Keywords Ponto-Caspian, Black Sea, Russia–Ukraine War, Ukraine, Dnieper River, Kakhovka Dam, Biodiversity, Habitat destruction, Flooding, Invasive species

Background

Biogeographic description and history of the Black Sea region

The biological diversity of the Black Sea region has a tumultuous biogeographic history entailing marked environmental changes and biotic adaptations to fluctuations in salinity conditions, temperature, and water levels (summarized by Zaitsev and Mamaev 1997; Zaitsev et al. 2002; Vinogradov et al. 2018). Major river drainages (west to east) in the northern Black Sea of Ukraine are the Danube, Dniester, Southern Bug, and Dnieper (also known as Dnipro) rivers (Fig. 1). Overall, the Black Sea's rivers introduce an average water volume of 391 ± 12 km^3/year, of which about one third escapes into the atmosphere and about two thirds exits into the Mediterranean Sea, with this water cycle and balance being very important to global climate change concerns (Stanev and Paneva 2001; García-García et al. 2022).

Water temperatures in the northern Black Sea coastal region are temperate, averaging about 3.3 °C in February to 24.1 °C in August (at Odesa, Ukraine; 46.4857°N, 30.7438°E) (Zaitsev and Mamaev 1997; Zaitsev et al. 2002). Salinities in the upper water layers of the Black Sea average 17–18 parts per thousand (ppt), and are lower near the mouths of the large rivers and in the Sea of Azov; many species in this region are euryhaline and highly adaptable to changing water quality and habitat conditions (see Zaitsev and Mamaev 1997; Zaitsev et al. 2002; Minicheva et al. 2010; Karsiotis et al. 2012; Vorobyova et al. 2017; Vinogradov et al. 2018; and references therein). Overall, the northern Black Sea ecosystem's marine, estuarine, and freshwater biota are characterized by long-term evolutionary and ecological acclimation to seasonal fluctuations in temperature, salinity, nutrient, and water flow regimes (summarized by Minicheva et al. 2010).

Permanent temperature, density, and salinity stratification characterizes the deeper areas of the southwestern Black Sea, due to the inflow of denser, higher salinity water from the Mediterranean Sea (Briggs 1974; Zaitsev and Mamaev 1997; Zaitsev et al. 2002; Poulos 2023). This deep area, which reaches 2212 m and comprises 88% of the Black Sea's volume, comprises a permanent layer of anoxic deeper water that does not mix, has high hydrogen sulfide content, is relatively stationary, and is inhabited by anaerobic organisms. The waters above this anoxic zone are less dense and much less saline, originating from the river flows. The Black Sea's sole outflow empties through the Bosporus Strait in northwestern Turkey near Istanbul into the Mediterranean Sea (Zaitsev et al. 2002; Poulos 2023) (Fig. 1).

Species endemism in the Black Sea stems from its long-term biogeographic history of spatial isolation, temperature differences from the Mediterranean fauna to the west, salinity barriers due to the freshwater influences, and the oxygen barrier in deep waters in the southwest (Briggs 1974; Zaitsev and Mamaev 1997). Specifically, the Black Sea basin has experienced a fluctuating geological and biogeographic history since the mid-Miocene Epoch (~ 15 Mya), including multiple pronounced sea-level changes and intermittent connections with the World Ocean, and associated inter-basin connections between the Black and Caspian Sea basins (Mandych 1995; Reid and Orlova 2002; Neilson and Stepien 2009a, 2009b; Stepien et al. 2013). These vacillating water levels and connections caused salinity levels to range 1–30‰ over the last 5 My (Reid and Orlova 2002), leading to biological lineage separations on multiple temporal scales (see Fleminger and Hulsemann 1987; Neilson and Stepien 2009a, 2009b, 2010; Brown and Stepien 2008; Stepien et al. 2013; Osikowski et al. 2016; Rewitz et al. 2015). The Black Sea region once contained an ancient and unique freshwater "Pontian" species assemblage, which then experienced an influx of marine species from the Mediterranean Sea (Briggs 1974; Zaitsev and Manaev 1997; Popov et al. 2004; Tkachenko 2024a, 2024b).

During the Pleistocene ice ages, the salinity of the Black Sea oscillated with the changing opening and closing of the Bosporus Strait connections (Zaitsev and Manaev 1997; Reid and Orlova 2002). Overall, the glacial advances induced periods of decreased salinity, and the interglacial periods experienced saltwater incursions. Today, the species richness of the Black Sea is relatively sparse compared to that of the Mediterranean Sea, containing only about one third as many species (Briggs 1974; Zaitsev et al 2002); however, about 25% of those in the Black Sea are endemic species or comprise divergent, distinctive populations (Briggs 1974); thus, this is a

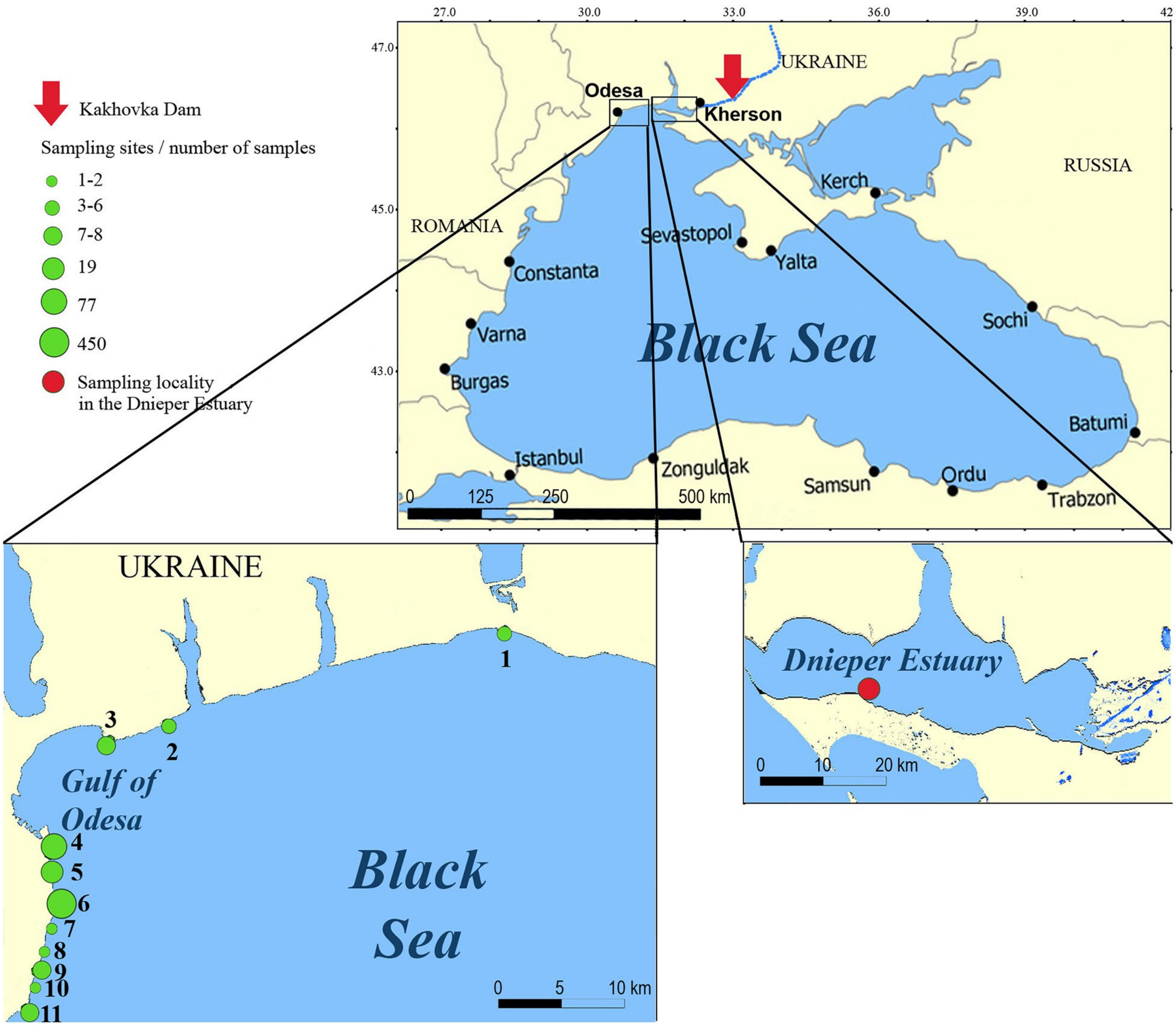

Fig. 1 Upper map shows the Black Sea, used with permission and attribution of the Nations Online Project (2024). Red arrow denotes the location of the Kakhovka Dam that was destroyed on June 6, 2023. **Lower left map** is adapted from Minicheva et al. (2023), indicating study points (in green) surveyed after the Kakhovka Dam's breakage and water release. Localities of sampling stations are numbered from east to west: (1) Kobleve (nearest the water release); (2) Fontanka; (3) Cape Pivnichny Odeskyi; 4) Cape Langeron; (5) Vidrada; (6) Cape Malyi Fontan; (7) Arkadia; (8) 10th station of Velykyi Fontan; (9) 13th station of Velykyi Fontan; (10) 16th station of Velykyi Fontan; (11) Cape Velykyi Fontan. **Lower right map** is adapted from Tkachenko et al. (2025), showing the site (in red) of the fish sampling study conducted in the Dnieper Estuary. Maps were modified by YK; geographic coordinates are in the text.

unique biological area. Moreover, the overall abundance of those species, primary productivity, and total biomass of the Black Sea biota are all much higher than those of the Mediterranean Sea (Zaitsev et al. 2002), rendering the region critically important to seafood supply and food webs.

Taxon representation and species diversity in the Black Sea today

Today's Black Sea's aquatic biota (encompassing marine, estuarine, and freshwater species) have four primary biogeographic heritages:

1) *Group 1*: Freshwater–euryhaline Pontian relict species that evolved in this region, which primarily inhabit the northern coast's river mouths, estuaries, and limans;

2) *Group 2*: Marine–euryhaline species of warm-temperate Mediterranean Sea origin that have become permanent residents, comprising about 80% of the Black Sea's contemporary species;
3) *Group 3*: Marine boreal relict species that are widely distributed in northern cold-temperate waters; and
4) *Group 4*: Invasive species (marine, euryhaline, and/or freshwater) that have been introduced anthropogenically—accidentally or intentionally—from other geographic regions, by passive or active transport through constructed canals, shipping and transport activities, ballast water releases, bait bucket transfers, fisheries stocking, aquaculture, or aquarium escapes, etc. (see Minicheva and Yeremenko 1993; Minicheva 2015; Stepien et al. 2005, 2013; Kvach and Kutsokon 2017; Dobrzycka-Krahel et al. 2023).

Group 1: Pontian heritage macrophytes in the Northern Black Sea region include the green algae (Phylum Chlorophyta) *Ulva intestinalis* and *U. maeotica* (Family Ulvaceae), *Chaetomorpha linum* and *Cladophora vagabunda* (Family Cladophoraeae); and the red algae *Bangia atropurpurea* (Phylum Rhodophyta, Family Bangiaceae), which species is highly invasive in many areas of the world. Zoological examples are: the zebra mussel *Dreissena polymorpha* and the quagga mussel *D. rostriformis* (Phylum Mollusca, Class Bivalvia, Family Dreissenidae); and the round *Neogobius melanostomus*, monkey *N. fluviatilis,* and tubenose *Proterorhinus semilunaris* gobies (Phylum Chordata, Class Actinopteri, Family Gobiidae) (see Stepien et al. 2005, 2013, 2010, 2009b; Brown and Stepien 2008; Neilson and Stepien 2009a). These dreissenid mussel and goby species have become invasive in other areas of Europe and elsewhere, facilitated by their broad adaptability to a wide range of temperatures, salinities, and habitats (Brown and Stepien 2008, 2010; Neilson and Stepien 2009a, 2009b; Manné et al. 2013; Roche et al. 2013; Stepien et al. 2013; Thiel et al. 2017).

Other Group 1 macroinvertebrate examples include: the unionid clams *Adacna laeviuscula* and *Monodacna colorata* (Phylum Mollusca, Class Bivalvia, Family Cardiidae); the freshwater bristle worm *Hypania invalida*, which has become invasive in much of Europe (Vučković et al. 2021) and the native euryhaline *H. kowalewskii* (both Phylum Annelida, Class Polychaeta, Family Ampharetidae); the amphipod *Pontogammarus robustoides* (Phylum Arthropoda, Subphylum Crustacea, Order Amphipoda, Family Gammaridae), which also is invasive in much of Europe (Bacela and Konopacka 2005); and the mysid shrimp *Paramysis kessleri* (Phylum Arthropoda, Subphylum Crustacea, Family Mysidae). Pontian heritage fishes (Phylum Chordata, Class Actinopteri) include the critically endangered Beluga sturgeon *Huso huso* and the stellate sturgeon *Acipenser stellatus,* which are both euryhaline (Order Acipenseriformes, Family Acipenseridae); the Black Sea sprat (also known as kilka) *Clupeonella cultriventris* (Order Clupeiformes, Family Ehiravidae), and several species of herrings in the genus *Alosa* (Family Clupeidae).

In general, these Pontian relict species often are adapted to both fresh and euryhaline waters, displaying high tolerances to shifting salinities and temperatures. For example, the round goby can readily tolerate abrupt alterations in salinities from 0 to 20‰ without acclimation, facilitating movement into new habitats (Karsiotis et al. 2012). Such broad environmental tolerances render many of these Pontian relict species highly adaptable to new and variable environmental conditions, leading to their successes as invasive species in other regions near and far (Arbačiauskas et al. 2013; Šidagytė and Arbačiauskas 2016; Copilaş-Ciocianu and Sidorov 2022; Paidere and Brakovska 2022; Dobrzycka-Krahel et al. 2023).

Group 2: Species having Mediterranean Sea origins constitute about 80% of those in the Black Sea today (Briggs 1987; Zaitsev and Mamaev 1997). Macrophytes include the brown algae *Gongolaria barbata* (Family Sargassaceae) and *Padina pavonica* (Family Dictyotaceae), and the red algae *Laurencia obtusa* (Family Rhodomelaceae) and *Gelidium crinale* (Family Gelidiaceae). Group 2 macroinvertebrates include most of the Black Sea's sponges (Phylum Porifera), jellyfishes (Phylum Cnidaria, Class Scyphozoa), polychaete worms (Phylum Annelida, Class Polychaeta), mollusks (Phylum Mollusca), and crustaceans (Phylum Arthropoda, Subphylum Crustacea), all of the echinoderms (Phylum Echinodermata), and more than 80 of the estimated 180 fish species (Zaitsev and Mamaev 1997; Yankova et al. 2014). The Mediterranean mussel *Mytilus galloprovincialis* (Class Bivalvia, Family Mytilidae) is listed as one of the "100 worst invasive species" by the Invasive Species Specialist Group of the International Union for Conservation of Nature (IUCN 2025a, b).

Among macroinvertebrates, only a few species of gastropods, echinoderms (Phylum Echinodermata), tunicates (Phylum Chordata, Subphylum Tunicata (= Urochordata), and barnacles (Subphylum Crustacea, Subclass Cirripedia) occur in the Black Sea; these taxa are much less diverse than they are in the Mediterranean Sea (Briggs 1974; Zaitsev and Mamaev 1997). Some Mediterranean Sea taxa have not become established in the Black Sea, including: radiolarian protists (Phylum Retaria, Subphylum Radiolaria) and pelagic foraminifera protists (Subphylum Foraminifera), and various groups of macroinvertebrates, encompassing:

stony corals (Phylum Cnidaria, Class Anthozoa, Order Scleractinia), siphonophores (Phylum Cnidaria, Class Hydrozoa, Order Siphonophorae), pteropod sea butterflies (Phylum Mollusca, Class Gastropoda, Order Pteropoda), scaphopod tusk snails (Phylum Mollusca, Class Scaphopoda), cephalopods (Phylum Mollusca, Class Cephalopoda), and brachiopod lamp shells (Phylum Brachiopoda) (Briggs 1974; Zaitsev and Mamaev 1997).

Many abundant Black Sea fishes trace to Mediterranean Sea origins, including the shore rockling *Gaidropsarus mediterraneus* (Family Lotidae), Roche's snake blenny *Ophidion roche*i (Family Ophidiidae), big-scale sand smelt *Atherina boyeri* (Family Atherinidae), and grass goby *Zosterisessor ophiocephalus* (Family Gobiidae) (Slastenenko 1956; Movchan 2011). Among pipefishes (Family Sygnathidae), the most numerous Mediterranean species in the Black Sea today are the euryhaline black-striped pipefish *Syngnathus abaster* and broadnosed pipefish *Syngnathus typhle*. Many blennies (Family Blenniidae), including several species of *Parablennius*, the subtropical sphinx blenny *Aidablennius sphyn*x, and the peacock blenny *Salaria pavo* are from the Mediterranean (Slastenenko 1956; Movchan 2011).

Marine mammals (Phylum Chordata, Class Mammalia, Order Cetacea) in the Black Sea today include three species of dolphins, which have been designated as divergent subspecies from their Mediterranean relatives—the bottlenose dolphin *Tursiops truncatus ponticus*, common dolphin *Delphinus delphis ponticus* (Family Delphinidae), and harbor porpoise *Phocoena phocoena relicta* (Family Phocoenidae)—and the monk seal *Monachus monachus* (Family Phocidae), which is on the verge of extinction (Zaitsev et al. 2002; Karamanlidis et al. 2023).

Group 3: Boreal relict cold-water marine macrophytes in the Black Sea include the red algae *Coccotylus brodiei* (Family Phyllophoraceae) and the brown algae *Ectocarpus siliculosus* (Family Ectocarpaceae); both are very widely distributed in many areas of the world. Black Sea boreal invertebrate species include the sea gooseberry comb jelly *Pleurobrachia pileus* (Phylum Ctenophora, Family Pleurobrachiidae) and copepods in the genera *Calanus* (Subphylum Crustacea, Order Copepoda, Family Calanidae) and *Pseudocalanus* (Family Clausocalanidae), which are very important members of the zooplankton and integral to fisheries food webs. Boreal origin fishes in the Black Sea are: the spiny dogfish *Squalus acanthias* (Phylum Chordata, Class Elasmobranchii, Family Squalidae); an endemic subspecies of sprat *Sprattus sprattus phalericus* (Class Actinopteri; Family Clupeidae), which has very high tolerance to hypoxia; an endemic subspecies of European flounder *Platichthys flesus luscus* (Family Pleuronectidae); an endemic subspecies of whiting *Merlangius merlangus euxinus* (Family Gadidae); and the Black Sea salmon *Salmo labrax* (Family Salmonidae) (Zaitsev et al. 2002).

Representation and trends of aquatic invasive species: Group 4

An invasive marine brown alga, *Halosiphon tomentosus* (= *Chorda tomentosa)* (Phylum Phaeophyta, Order Laminariales, Family Halosiphonaceae) was described from the Northwestern Black Sea region of Odesa, Ukraine in 2015; it originally inhabited the Atlantic coasts of North America and Europe (Minicheva 2015). Another brown alga, the stringy acid kelp *Desmarestia viridis* (Family Desmarestiaceae) is invasive in the Black Sea as well as many other areas of the world. That species destroys itself and other marine plants when damaged, which is believed to comprise a defense against herbivory (Gagnon et al. 2006).

Invasive macroinvertebrate species long-ago introduced to the Black Sea marine habitats from North American coastal waters include the following crustaceans: the bay barnacle *Amphibalanus improvisus* in ~ 1844 and the ivory barnacle *Balanus eburneus* (both in Family Balanidae); the Zuiderzee crab *Rhithropanopeus harrisii* (Family Panopeidae) in ~ 1938, which inhabits fresh–brackish waters and is broadly distributed throughout much of Europe; and the predatory blue crab *Callinectes sapidu*s (Family Portunidae) in ~ 1967 (Zaitsev and Mamaev 1997; Gomoiu et al. 2002; Kideys 2002). The sea walnut ctenophore *Mnemiopsis leidyi* (Family Bolinopsidae), is another high-impact invader from North America; it first appeared in the Black Sea in 1982, likely originated from ships' ballast water releases, and decimated native populations of zooplankton, fish larva, and anchovies. The soft-shell clam *Mya arenaria* (Class Bivalvia, Family Myidae), also originated from North America, appearing about 1966 in Odesa; this species outcompetes native bivalves (Gomoiu et al. 2002; Kideys 2002; Zaitsev et al. 2006).

Invasive species that originated from other regions of the world include the polychaete worm *Mercierelle enigmatica* (Family Serpulidae) from India and the rapa whelk *Rapana venosa* (Class Gastropoda, Family Muricidae) (Zaitsev and Mamaev 1997; Gomoiu et al. 2002; Hulak et al. 2022). The rapa whelk is a voracious predator of native mussels, clams, and oysters. It originally was from the Sea of Japan and first appeared in the Northern Black Sea in 1946 (Gomoiu et al. 2002; Hulak et al. 2022).

Among fishes, the fresh–brackish water pumpkinseed sunfish *Lepomis gibbosus* (Family Centrarchidae) was intentionally introduced; it originally was from North America and likely spread into the Black Sea from other invasive populations in Central Europe (Khutornoi et al. 2023; Dudliv et al. 2024). The pumpkinseed sunfish feeds on fish eggs, resulting in declines of native fish populations, and has become abundant in the Odesa region. Other intentionally introduced fishes are: the mosquitofish *Gambusia affinis* (Family Poeciliidae), which arrived in 1925 from Italy and has become widely prevalent in nearshore Black Sea marine, estuarine and freshwaters; and the commercially-fished haarder *Planiliza haematocheilus* (Family Mugilidae) that came from Asia in 1990, and reaches 1 m in length (Zaitsev and Mamaev 1997; Kvach and Kutsokon 2017). The Chinese sleeper *Perccottus glenii* (Family Odontobutidae) is a voracious predator on other fishes; it was originally from Asia, and Ukraine has become a center for its spread in Europe (Kvach et al. 2016, 2022; Grabowska et al. 2020).

In turn, due to construction of canals, global shipping, and ballast water releases, many aquatic species that originally were native to the Black Sea region have become invasive in other areas of the world, including in North America (see Cristescu et al. 2004; Stepien et al. 2005, 2013, 2009b; Neilson and Stepien 2009a). Examples are: the zebra and quagga mussels, the scud amphipod *Echinogammarus ischnus* (Family Gammaridae), and round and tubenose gobies. Their histories of adaptiveness and ecological plasticity attributed to historic fluctuations in salinities and temperatures experienced in the Black Sea region likely have predicated their invasive successes (summarized by Stepien et al. 2013; Dobrzycka-Krahel et al. 2023).

An analysis by Dobrzycka-Krahel et al. (2023) examined invasive macroinvertebrates, which originated from the Black Sea and the overall Ponto-Caspian region, finding that: (A) 27% of them exclusively inhabit the marine adaptive zone (salinities of 0.5–35‰), (B) 25% are entirely freshwater (salinities of 0–0.5‰), (C) 45% are euryhaline (salinities from 0 to 35‰), and (D) 3% are semi-aquatic and terrestrial. Across the world, euryhaline aquatic invasive species (AIS) that were native to the Ponto-Caspian region (45%) have been very successful invaders, significantly outnumbering those originating from other regions of the world (7.5%), whose environmental tolerances likely have pre-adapted them for widespread establishment in harbors, estuaries, and coastal areas. Moreover, most (70%) of the Ponto-Caspian origin invertebrate aquatic invasive species have freshwater-tolerant populations (B + C), rendering them very successful invaders of inland water bodies. These broad salinity tolerances of Ponto-Caspian aquatic invasive macroinvertebrates underlie their tremendous invasion successes and growing neocosmopolitan distributions through human-mediated dispersal (Dobrzycka-Krahel et al. 2023).

Ecology, pollution, habitat, and biodiversity before the War

The Northern Black Sea region's biodiversity and habitats have suffered tremendously from the ongoing anthropogenic effects of eutrophication due to agricultural run-off of nutrients and fertilizers; pollutants, including pesticides, oil, and heavy metals from industry; insufficiently treated sewage, and storm water and agriculture run-off; fisheries exploitation and destruction of the benthic community from dragging trawls and dredges; and invasive species introductions and spread (summarized by Bakan and Buyukgungor 2000; Kideys 2002; Zaitsev et al. 2002; Alexandrov et al. 2017; Stevens et al. 2019). Overall environmental quality, and toxin and eutrophication levels, had gradually improved after the collapse of the Soviet Union and greater ecological protection in the two decades prior to the Russia–Ukraine War (summarized by Kideys 2002; Stevens et al. 2019).

By 2021, 13% of Ukraine's land and nearly 10% of its waters were protected in some form, which scientists and nature advocates were actively working to increase prior to the Russia–Ukraine War's outbreak (Marciano 2023). Ukraine's important coastal and marine ecological areas include 22 Ramsar Sites under the Ramsar Convention on Wetlands (Ramsar 1971) covering 750,521 ha of wetlands, numerous terrestrial Protected Areas (PAs), as well as 45 designated Marine Protected Areas (MPAs). Eleven of those MPAs were lost after Russia's annexation of the Crimea in 2014. Yet, Ukraine's MPAs cover just 1.3% of its total marine area, and the status of that protection has been rated as poor by the Conflict and Environment Observatory (CEO 2023). There have been high levels of illegal, unreported and unregulated fishing in the Black Sea, augmenting weak fisheries governance (CEO 2023).

Comprising a major Ukraine resource, habitat, and nursery area for the Black Sea, the extensive Dnieper–Bug Estuary area (Fig. 1) is characterized by small islands, riparian forests, shallow water zones, and extensive reed beds, which has been protected and designated as a wetland of international importance under the Ramsar Convention on Wetlands (Ramsar 1971). The Dnieper–Bug Estuary contains brackish waters, which in recent decades have varied from a salinity of 1.0–3.3‰ in the east (close to the Dnieper River's mouth), to about 1.0–6.0‰ in the central part, and up to 11.0‰ in the west (Ilyin 2023).

The Kakhovka Hydroelectric Power Plant was located 60 km upstream of the city of Kherson, Ukraine (46.6354°N, 32.6169°E) (Fig. 1); it was constructed under the former Soviet Union in the 1950s (Gleick et al. 2023). Its primary purpose was to provide hydropower, and secondarily, reliable irrigation water and drinking water supply for southern Ukraine from its Dam and Reservoir. The Dam's completion in 1956 led to a 22% decrease in freshwater outflow into the Dnieper–Bug Estuary (Zalumi 1967). In recent years prior to June 2023, the Dnieper River's average water outflow near its mouth had dropped by around 10 km^3 per year (from a previous flow of about 1690 m^3/s or 53 km^3 per year), due to anthropogenic water withdrawals and increased evaporation (Vyshnevskyi et al. 2023; Gleick et al. 2023).

The wetlands of the Dnieper–Bug Estuary region have comprised important breeding areas for many endangered species, containing the largest great white pelican colony *Pelecanus onocrotalus* (Class Aves, Family Pelecanidae) and the squacco heron *Ardeola ralloide*s (Family Ardeidae), as well as the river otter *Lutra lutra* and the endangered European mink *Mustela lutreola* (Class Mammalia, Family Mustelidae). This area also has provided an important source of clean drinking water. During the past decade, the region has experienced a serious problem with groundwater salinization, due to intensive nearby agricultural irrigation (Krumenacker 2023).

A decade of surveys prior to the War have revealed that the fish fauna of the Dnieper–Bug Estuary comprised about 53 species, 18 of which are commercially important, including the Black Sea sprat *Clupeonella cultriventris* (Family Ehiravidae) and the invasive Prussian carp (i.e., gibel) *Carassius gibelio* (Family Cyprinidae) (Verlatiy et al. 2009; Geina 2019; Tkachenko 2023; Tkachenko et al. 2025). During the last decade, 22 marine/brackish water fish species were documented in the Dnieper (Dnipro) Estuary proper in long-term surveys conducted by Tkachenko (2023) and Tkachenko et al. (2025). After 2004, six Mediterranean marine fish species additionally appeared and were recorded in those surveys: the common stingray *Dasyatis pastinaca* (Family Dasyatidae); the endangered brown meagre *Sciaena umbra* and the Shi drum *Umbrina cirrosa* (both in Family Sciaenidae); the white seabream *Diplodus sargus* and the gilt-head bream *Sparus aurata* (both in Family Sparidae); and the tub gurnard *Chelidonichthys lucerna* (Family Triglidae) (Tkachenko 2023; Tkachenko et al. 2025).

Prior to the June 2023 Kakhovka Dam's water release, an increasing preponderance of marine jellyfishes and ctenophores were documented in the Dnieper Estuary due to its increased salinity, encompassing: the moon jellyfish *Aurelia aurita* (Family Ulmaridae), barrel jellyfish *Rhizostoma pulmo* (Family Rhizostomatidae), the invasive sea walnut *Mnemiopsis leidyi* (Family Bolinopsidae), and the invasive pink slipper comb jelly *Beroe cucumis* (Family Beroidae) (Tkachenko 2023; Tkachenko et al. 2025). From 2020 to 2023, shrimp fisheries for the brackish native species Baltic prawn *Palaemon adspersus* and the native rock shrimp *P. elegans* (Family Palaemonidae) were being developed in the Dnieper Estuary (Tkachenko 2023; Tkachenko et al. 2025). This region now has become markedly affected by the War and the breakage of the Kakhovka Dam, with its massive release of freshwater and contaminants on June 6, 2023 (see Results below).

Studying the effects of the ongoing War on Black Sea biodiversity

The Russia–Ukraine War has been the largest scale Europe war since World War II (1939–1945), with the recent invasion and escalation commencing in February 2022; estimates indicate that over 30% of Ukraine has been contaminated with landmines and unexploded ordnance to date, and there has been over $56.4 billion U.S. in environmental damage (Hryhorczuk et al. 2024). Landscape destruction, shelling, wildfires, deforestation, and pollution have adversely affected ~ 30% of Ukraine's Protected Areas (PAs) (Hryhorczuk et al. 2024). As a result of the War, over 20.7 billion cubic meters of wastewater have been discharged into surface waters, leading to widespread pollution (Krumenacker 2023), whose ecological effects remain largely unstudied.

Primary impacts of the Russia–Ukraine War on aquatic ecosystems and biodiversity in the Black Sea region have encompassed increased chemical, debris, munition, and acoustic pollution, and physical damage to habitats, the curtailment of conservation activities, and decreased commercial fishing and tourism (see Sousa et al. 2022; Pereira et al. 2022; Krumenacker 2023). For example, in the Tuzly Estuaries National Nature Park south of Odesa, located between the Danube and the Dniester Rivers (45.7833°N, 30.0000°E), by May 2022 an estimated 2500 dead dolphins were reported to have washed ashore, which some researchers attributed to acoustic trauma from submarine sonar (Marciano 2023; Hryhorczuk et al. 2024). However, some other scientists have questioned the cause of these strandings (Vishnyakova et al. 2023).

The overall anthropogenic consequences of the Russia–Ukraine War on the Black Sea ecosystem can be classified as having either negative or positive overall effects on biological diversity and habitats, which sometimes interact in concert and include:

1) *Negative ecological effects* are damages that are associated with military operations. These range from artillery and missile fire, mining and explosives, ship and aircraft wrecks and debris, uncontrolled fires and washout of combustion products, damage to vegetation and habitats, and acoustic effects on dolphins

and fishes. Chemicals from warfare that enter aquatic food webs include petroleum and by-products from oil spills and heavy metals, such as lead (Pb). These are prevalent in military equipment and usually are long-lasting in the environment. Many of the negative effects are readily transmitted along the extensive Black Sea coastline through water currents, waves, and upwellings. Other deleterious ecological effects result from cessation of Terrestrial and Marine Protected Areas (PAs and MPAs, respectively), and non-observance by military water transport of the rules for seawater exchange of ballast water, which can lead to transport and outbreaks of invasive species.

2) *Positive ecological effects* stem from decrease in the intensity of anthropogenic impacts on habitats and communities. These include recovery of native species and fishery stocks and their habitats due to closures of beaches, commercial and recreational fishing, commercial shipping traffic, and recreational boating; fewer people (visitors, tourists, and residents) recreating in beaches and parks; cessation of shoreline building and construction; and reduced dumping in waters, etc. The War has offered an unprecedented experiment involving the depopulation of a long coastline due to mining and access prohibition by military authorities (see Fig. 2). These factors have acted to restore the life cycles, habitats, food webs, and natural behavior of a large number of nearshore organisms, including coastal zone vegetation, seabirds, other vertebrates, and invertebrates.

The relative strengths of the negative and positive impacts on the ecosystem as a result of the War also depend on their timing occurrences with annual and seasonal climatic and weather conditions. Climate anomalies can worsen or improve overall ecological responses of biological communities, as well as affect the survival, recruitment, and continuity of populations.

Approach

Our review paper summarizes and interrelates the findings from four primary research studies, termed *Studies I–IV*, which were led by scientists from this authorship team from the Institute of Marine Biology (IMB) of the National Academy of Sciences of Ukraine (NASU), and focus on the various ecological effects of the Russia–Ukraine War on aquatic communities in the Northwestern Black Sea Region (NWBSR) (Figs. 1 and 2). We integrate the results in a broader ecological context in relation to other investigations from the literature, examining the overall short- and longer-term negative and positive impacts of the War on marine, estuarine, and freshwater biota and their habitats. We aim to provide foundational knowledge for future and further in-depth analyses.

The four studies, which are summarized and interrelated here are: ***Study I*** documents the widespread occurrence of oil spills from military action early in the War using satellite imagery in 2022, prior to the Kakhovka Dam's breakage, including their extent in MPAs (Minicheva and Sokolov 2024). ***Studies II and III*** focus on the biotic and habitat effects caused by the June 6, 2023

Fig. 2 View of Odesa, Ukraine beach, with warning sign, Gulf of Odesa, Black Sea, in October 2022

destruction of the Kakhovka Hydroelectric Power Plant (46.7786 N, 33.3697 E; see Fig. 1 map) on the Dnieper River, which released a tremendous flood of freshwater into the Dnieper-Bug Estuary and the NWBSR, constituting the most profound ecological impact of the War to date. ***Study IV*** examines the overall effects of the War on the benthic macrophyte community.

Studies II and III examined ecological effects just after the Kakhovka Dam's breakage, which caused a flood of 19.9 billion cubic meters of freshwater and pollutants into the NWBSR, swamping 77 settlements and more than 100,000 hectares (247,000 acres) of agricultural lands, nature parks, and forests. Mud at the bottom of the Kakhovka Reservoir contained decades of industrial waste from the city of Zaporizhzhia (47.82289°N, 35.19031°E) in southeast Ukraine, including large amounts of heavy metals, which were released by the Dnieper River's current into the water column and distributed downstream. The Dnieper River discharge was polluted with over 150 tons of machine oil, large amounts of organic wastes, and an unknown number of landmines that were dislodged by the flood waters; much of these were carried downriver into the estuaries and out to the Black Sea (Glieck et al. 2023; Hryhorczuk et al. 2024). This catastrophic flooding and destruction throughout the lower Dnieper River and Southern Bug River Estuary region exerted extensive effects on marine and aquatic species and their habitats throughout the NWBSR (Krumenacker 2023; Glieck et al. 2023; Hryhorczuk et al. 2024).

The freshwater outflow reached the northern Black Sea about two days later on June 8, 2023 (Krumenacker 2023). Our review paper overviews the known results of the Kakhovka Dam's release on the NWBSR ecosystem, whose findings were originally reported by Minicheva et al. (2023) for Study II and by Tkachenko et al. (2025) for Study III (publications are in Ukrainian), which are summarized here in English and placed in broader ecological context.

Study IV presents new unpublished data by GGB, which examine the overall trends and patterns in the offshore benthic macrophyte (also known as phytobenthos) community (these include the macroalgae, or "seaweed", as well as angiosperm seagrasses) over time, both prior to and throughout the course of the War.

All four studies are situated in the NWBSR of Ukraine, analyzing conditions and changes in marine and aquatic habitats that influence biodiversity. Results from Studies I–IV are discussed here in the context of overall effects, positive and negative, on marine, estuarine, and freshwater biota. The purpose of our review paper is to serve as a baseline record to inspire further and future analyses. We anticipate an updated review paper after the end of the War.

Methods and analyses: effects of the ongoing War on Black Sea biodiversity

Methods for analyzing the occurrence of oil spills (Study I)

The occurrences of oil spills due to military activity for the first six months of the War in 2022 were analyzed from satellite imagery by the IMB (headed by GGM), comprising 31 cases (images) of oil spills on the waters of the NWBS (Fig. 3). These covered a total area of 4711.6 km^2 (including overlap areas on different dates), which constituted 16.2% of the NWBS. The total area that lacked data on the various imagery dates was 4354.98 km^2, comprising 14.9% (Minicheva and Sokolov 2024; Fig. 3). This study aims to provide comparative data for future analyses of the effects of oil spills from the War, with further studies pending until there is safe access to these sites.

Methods for analyzing the effects of the Kakhovka Dam's water release (Study II)

(reported by Minicheva et al. 2023 in the Ukrainian language, and adapted here)

On June 6, 2023, IMB researchers undertook a research expedition to record the "zero" state—the starting point of the Kakhovka Dam disaster as it reached the Black Sea. The NWBS coast was monitored and sampled from the Sukhyi Estuary (also known as Liman) (46.3177°N, 30.6703°E) near Odesa (to the west, site 11 on Fig. 1 lower left map) to the Tylihul Estuary (46.8434°N, 31.1249°E) near Kherson, at the outflow of the Dnieper River Estuary (site 1 on Fig. 1, lower left map).

Data collections included SCUBA diving observations and videos through August 24, 2023, from 11 stations along the coast (see Fig. 1, lower left map). The Dnieper River's flow data were obtained from the weather station at Ochakiv (46.6188°N, 31.5388°E), located on the banks of the Dnieper Estuary. Seawater temperature and salinity were obtained for three weeks prior to the arrival of the contaminated water (May 15, 2023–June 6, 2023) and for three weeks after the return of salinity values to normal (June 24, 2023–July 15, 2023), as provided by the Ukraine Ministry of Health for the city of Odesa (46.4857°N, 30.7438°E).

Water samples, temperature, salinity, dissolved oxygen (mg/dm^3), and % oxygen saturation were analyzed using standard IMB laboratory methods. Lethal dose (LD)-50 toxicity tests were conducted on saline-adapted cladoceran *Daphnia magna* (Subphylum Crustacea, Class Brachiopoda, Family Daphniidae) cultures in comparison to controls. Indicators of the concentration of chlorophyll-a were obtained using the following international platforms: "Copernicus Marine Service—CMEMS" (CMS 2023), with the "Black Sea Ocean Color Plankton MY L4" (Kajiyama et al. 2018), processing products of

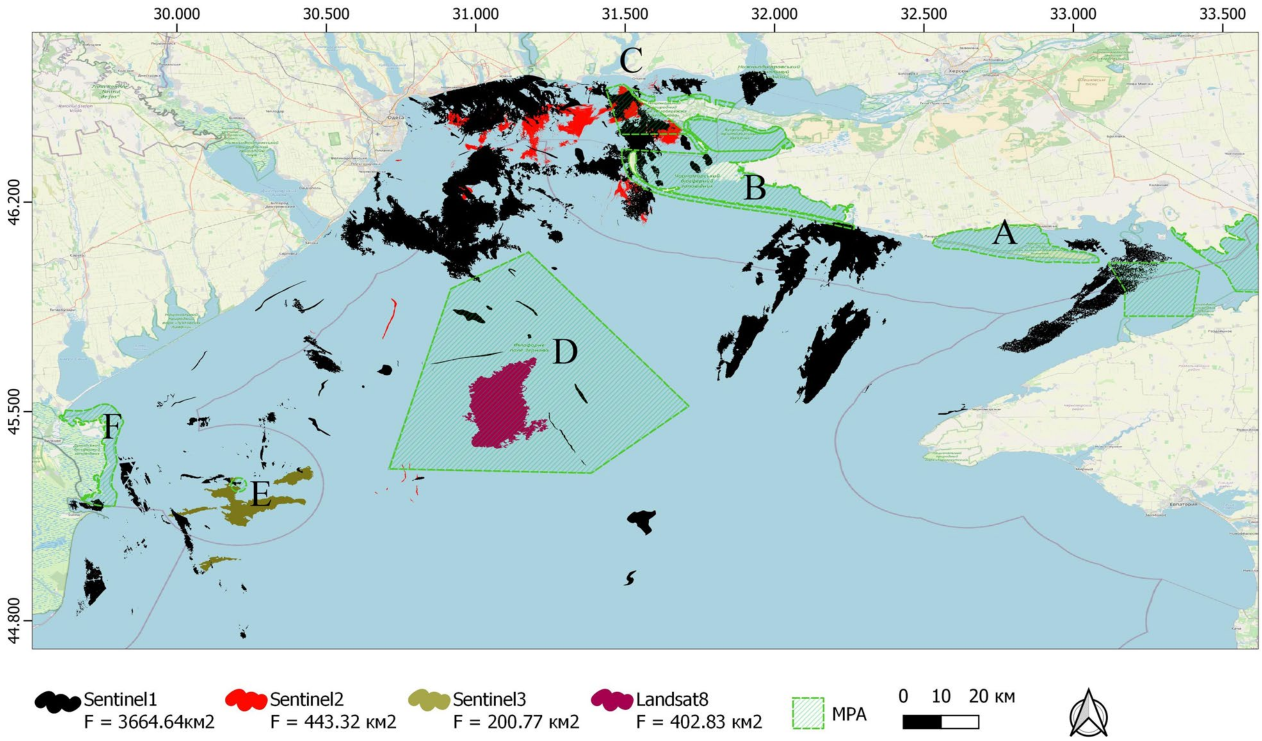

Fig. 3 Identified oil spills in 2022, within the boundaries of the Ukrainian sector of the NWBS, based on satellite imagery from optical images and radar (Study I; adapted by YK from Minicheva and Sokolov 2024). **A** Karkinitskiy Reserve; **B** Black Sea Biosphere Reserve; **C** Beloberezhia Sviatoslava National Park; **D** Zernov's *Phyllophora* Field; **E** "Zmiinyi Island" Reserve; and **F** Danube Biosphere Reserve

the Sentinel-3 satellites (OLCI) and Aqua (MODIS) in the optical ranges of the survey, and using the bio-optical neural network processor C2RCC (Brockmann et al. 2016) with the Sentinel Application Platform (SNAP; version 9.0, 2024) software package.

Biological samples were collected and analyzed, employing IMB standard methods, encompassing the:

1) *Microbenthos community*, measuring < 0.1 mm in size, comprising bacteria, diatoms, ciliates, amoebas, and flagellates from the upper layer of the sand sediment at 0.5 m depth, with taxon abundances calculated per 1 m^2;
2) *Meiofauna community* from the sand or mud benthos, containing small invertebrates such as molluscs, worms, and crustaceans (including benthic copepods), sampled with three sediment replicates at 5 cm depth using a hand corer, which then were filtered with a 1.0 mm-mesh sieve, and the taxon abundances calculated per 1 m^2;
3) *Benthic macro community*: Macroinvertebrates (i.e., zoobenthos) and macrophytes (i.e., phytobenthos, encompassing macroalgae or "seaweeds", plus seagrasses and other flowering plants) sampled from the hard substrate in 10 × 10 cm quadrats, and the taxon abundances were calculated per 1 m^2;
4) *Phytoplankton* from 1 L of surface water, whose abundances were calculated per 1 m^3; and
5) *Zooplankton*, which were sampled by filtering 100 L of water from the surface layer or with a vertical plankton tow, both using a 100 µm mesh net, with abundances calculated per 1 m^3.

Processing of the samples followed the IMB's standard sampling and analysis methods and procedures. Macrophyte surface index calculations were made according to Minicheva et al. (2003). Plant nomenclature was based on AlgaeBase (Guiry and Guiry 2024), and animal nomenclature followed the World Register of Marine Species (WoRMS 2024).

Mortality of the Mediterranean mussel *M. galloprovincialis*, which is a resource species and ecosystem engineer in the region, was determined and individuals were measured with a caliper and weighed (g). To calculate the total number and biomass of dead mussels, the area of the NWBS that came under the intense influence of freshwater and the amount of hard substrate habitat were determined according to Landsat 8–9 satellite data in reference to the Open Geospatial Consortium (OSG 2024).

To quantitatively compare the effects of the water released by the Kakhovka Reservoir on the abiotic factors and on the aquatic taxa, the values of the respective indicators on specific sampling dates (from June–August 2023) were calculated in comparison to their regional norms, as determined for several previous decades, as: $A = (P_i - P_x)/P_x \times 100$, where: A was the anomaly (%); P_x was the value of the regional norm; and P_i was the value for the period of June–August 2023.

Methods for analyzing the effects on the fish community of the Kakhovka Dam's release (Study III) *(reported by Tkachenko et al. 2025 for June 2023 sampling in the Ukrainian language, and adapted here)*

Fishes were sampled in the Dnieper River Estuary near the village of Vasylivka (46.5292°N, 31.7956°E) at depths of 0.5–0.6 m in June 2023, following sampling protocols and with equipment used there for monitoring over the previous 5–10 years (Tkachenko 2023; Tkachenko et al. 2025) (Fig. 1). This locality was characterized by a sand-mud bottom, with 90–100% macrophyte coverage by the hornwort *Ceratophyllum demersum* (Family Ceratophyllaceae) extending to 25 m from the coast line, which then decreased to 40–60% coverage at 25–175 m from the coast line. Because the study reported here took place during Russian occupation of the region, when fisheries research was prohibited by the Occupation administration and the south shore of the Estuary was extensively mined, the 2023 investigation reported here was confined to what could be sampled using available fishing gear:

1) Shrimp fyke-nets: 24 m length, 0.4 m height; 8 mm mesh in the main part and 6.5 mm in the wings; and
2) Gill-nets (four nets of different types): 50 m length, 1 m high (two nets) and 1.5 m high (two nets); mesh diameters of 32 mm, 40 mm, 65 mm, and 75 mm, respectively.

All nets were installed overnight until 05:00–07:00, except for the 65 mm and 75 mm mesh nets, which were deployed from 06:00–16:00. The fyke-nets were installed daily until June 6, 2023 (the day of the Dam's breakage); the gill-nets were deployed every 2–4 days depending on weather conditions. From June 7–13, 2023, fishing was not possible due to the hazardous high-water levels, fast current, and floating debris after the Kakhovka Dam's breakage (e.g., from June 8–9, 2023, water levels were 0.85 m above normal).

Fishes were identified to the species level, using taxonomic keys by Kottelat and Freyhof (2007) and Movchan (2011), and numbers of individuals of each species and their total lengths (TL, cm) were recorded. Since the fishes of commercial size were needed by local people for food, representative smaller individuals of each species were preserved in 4% formalin as voucher samples. Salinity was not measured due to lack of equipment, and changes in the habitats were limited to visual observation. Findings were compared with data from 10 years of fish collections made at the same sites, using the same equipment and the same methods (Tkachenko 2024a, 2024b).

Methods for analyzing changes in the benthic macrophyte community before and during the War (Study IV) *(new unpublished results by GGM)*

Study IV evaluates the overall trends and patterns in the nearshore benthic macrophyte (i.e., seaweeds, encompassing the macroalgae and seagrasses) community along the NWBSR over time, both prior to and throughout the course of the War to date. Macrophytes were identified to the level of genus, with prevalent genera including red algae: *Chondrus* (Family Gigartinaceae), *Lithophyllum* (Family Lithophyllaceae), *Corallina* (Family Corallinaceae), *Phyllophora* (Family Phyllophoraceae), *Ceramium* (Family Ceramiaceae), *Callithamnion* (Family Callithamniaceae), *Gelidium* (Family Gelidiaceae), *Bangia* (Family Bangiaceae), and *Acrochaetium* (Family Acrochaetiaceae); brown algae: *Cystoseira* (Family Sargassaceae), *Dilophys* and *Padina* (both in Family Dictyotaceae), *Ectocarpus* (Family Ectocarpaceae); green algae: *Chaetomorpha* and *Cladophora* (both in Family Cladophoraceae), *Ulva* (Family Ulvaceae), and *Bryopsis* (Family Bryopsidaceae); and the flowering seagrass *Zostera* (Phylum Tracheophyta, Superclass Angiospermae, Family Zosteraceae) (see Minicheva 2013). This macrophyte community comprises the basis for primary production and habitat biomass, supporting fish, invertebrate, detritivore, and epiphytic community members with food web energy and a 3-dimensional place to live.

Morphofunctional indicators are used as standards to assess the Ecological Status Class (ESC) of the Black Sea's coastal ecosystem (following the guidelines of Minicheva 2013) in accordance with requirements of the Marine Strategy Framework Directive (MSFD 2008), comparing the pre-War years with the War period to date. The average species ecological activity index for the macrophyte community, S/Wx, is used to characterize the intensity with which macrophyte species participate in the overall primary production process (Minicheva et al. 2003; Minicheva 2013). Its value decreases during favorable weather and climate conditions, and also decreases with lessened anthropogenic load.

The Surface Index (SI) is another morphofunctional indicator, which characterizes the intensity of the autotrophic process by the phytoplankton community in coastal marine ecosystems (Minicheva et al. 2003). Five classification categories are used for the ESC, ranked from “Bad” to “High” in overall environmental quality, in accordance with the requirements of the Water Framework Directive (WFD 2000).

Results from the four studies (I–IV) are discussed in the context of overall effects of the War, both positive and negative, on marine, estuarine and freshwater biodiversity. Our review paper aims to serve as a baseline record to inspire further and future analyses.

Results and discussion

Ecological effects on habitats due to the Russia-Ukraine War

Influence of weather and climate, coupled with closures of fisheries, boating, and beaches

The ongoing Russian invasion of Ukraine began on February 26, 2022, whose first year was influenced by unseasonably dry conditions in the NWBSR, with precipitation 2.5 times lower than the long-term regional normal level, and moderate water and air temperatures. This led to environmentally favorable conditions for most aquatic life. Throughout the War, the long Ukraine coastline of the NWBSR (Fig. 1) has experienced significantly reduced recreational and commercial impacts, since people have been prohibited from access. The ecological impacts on the coastal zone and its species thus have been lessened, with positive effects on marine, estuarine, and freshwater species. Restorative plant succession has occurred on sandy beaches, and coastal flora, fauna, and seabirds have rebounded in nearshore and offshore aquatic habitats (Fig. 2).

Oil spills and Marine Protected Areas (MPAs), Study I (adapted from Minicheva and Sokolov 2024)

The occurrences of oil spills due to military activity were analyzed from satellite imagery in 2022 (Fig. 3). The team documented 31 cases (images) of oil spills on NWBS waters, covering a total area of 4711.6 km^2 (including overlap areas on different dates), which constituted 16.2% of the NWBS area. The total area lacking data on various imagery dates was 4354.98 km^2, which was 14.9% (Fig. 3).

The percentage of sea surface area that was covered by oil spills in the MPAs along the NWBS, from February–September 2022, was calculated as: (A) 25% of the Karkinitskiy Reserve (45.4573°N, 35.8371°E)**;** (B**)** 16% of the Black Sea Biosphere Reserve (46.5375°N, 32.5393°E); (C) 67% of the Beloberezhia Sviatoslava National Nature Park (46.4986°N, 31.6780°E); (D) 21% of the Botanical Reserve of the National Significance “Zernov’s *Phyllophora* Field” (45.5167°N, 31.1778"E); (E) 62% of the Zoological Reserve of the National Significance “Zmiinyi Island” (45.2543°N, 30.2045°E); and (F) 5% of the Danube Biosphere Reserve (45.3965°N, 29.6686°E). Thus, MPAs were tremendously affected, significantly influencing the macrophyte community, primary productivity, and benthic habitats. Notably, site D, “Zernov’s *Phyllophora* Field” is a unique habitat with a dense stand of red algae (Family Phyllophoraceae), housing a high diversity of associated fauna (Revkov et al. 2018). In 2008, this area was declared a national botanical reserve in Ukraine to protect and restore its unique natural environment, comprising the first offshore, fully marine MPA in the Black Sea. It also is the largest MPA, with a total area of 402,500 ha, covering 12.5% of the NWBS shelf. This MPA has nine species of algae, fishes, and crustaceans that are on the International Union for Conservation of Nature and Natural Resources (IUCN) European Red List of Threatened Species (see https://www.iucnredlist.org/regions/european- *red-list*) (IUCN 2025b), rendering its habitat highly vulnerable to effects of oil spills and the War (Kostylev et al. 2010; Revkov et al. 2018). Further studies by IMB researchers are planned, pending safe access to these MPA areas.

Freshwater and pollutants released from the Kakhovka Dam break, Study II

(adapted from Minicheva et al. 2023)

Water was released from the Kakhovka Reservoir for 17 days; the Reservoir’s original volume was 18.2 km^3, which emptied by 73% (Ukraine Ministry of Environment)—equivalent to 13.3 km^3. The average annual runoff volume from the Dnieper–Bug Estuary from 1977–2020 was estimated as 43.4 km^3. Over 10 days, from June 7–17, 2023, 31% of the average multi-year volume of annual runoff reached the Black Sea, totaling + 425% of the normal yearly volume; volumes were + 650% at the first impact, and + 170% afterwards. These data and results from Minicheva et al. (2023) are summarized in Table 1.

Temperature effects

Just before the arrival of contaminated water released from the Kakhovka Reservoir, the sea surface water temperature at the port of Odesa (Odesa-Port MSS) was 19.3 °C. From June 6–24, 2023, sea surface water temperature was > 21.6 °C; from June 25–July 15 the sea surface water temperature was > 20 °C. Thus, surface sea water temperature values showed no significant anomalies.

Salinity effects

Daily seawater salinity at station 4 showed that the fresh, warm water outflow from the Kakhovka Reservoir arrived on June 9, 2023, significantly lowering surface salinity from 13‰ on June 6 to 7.4‰ on June 9. The lowest salinity—3.95‰—was recorded on June 11, which gradually increased to 15‰ by June 26. From July–August 2023,

Table 1 Anomalies (% change from seasonal averages) of abiotic factors and biological community responses to the Kakhovka Dam's water releases to the Northwestern Black Sea marine ecosystem in summer 2023 (Study II).

Impact stage		**1st stage (June 6–11, 2023)**	**2nd stage (June 12–July 10, 2023)**	**3rd stage (July 11–August 10, 2023)**	**4th stage (August 11–31, 2023)**
Ecosystem response		**Hydrological, chemical and physical impacts**	**Biological community response**	**Continuing high biological response**	**Return to average seasonal, regional levels**
Abiotic factors	Riverine inflow	650	170	< 10	< 10
	Salinity	71	15	< 10	< 10
Marine communities	Phytoplankton	450	1400	> 10	< 10
	Zooplankton	< 10	900	> 10	< 10
	Macrophytes	< 10	> 10	90	< 10
	Zoobenthos	< 10	1600	900	400

salinity on the Odesa coast varied from 10–17‰, which are normal levels during the summer. Thus, salinity quickly returned to average regional conditions following the Dam's water release (see Table 1).

Water quality, nutrients, and pollutants

The influx of polluted water arriving from the Kakhovka Reservoir contained high levels of suspended and dissolved mineral and organic substances, which affected the seawater quality adjacent to the Dnieper Estuary. Surface waters off Odesa had a salinity of 4‰, and oxygen saturation was less than 75%, which both were much lower than normal seasonable levels. Levels of nitrites and nitrates, used by algae for photosynthesis, were at average levels, and did not exceed the maximum permissible concentration (MPC) levels (Shypotilova et al. 2021) for pollutants in nearshore seawaters of Ukraine. In surface waters along the Odesa coast from June 9–13, 2023, salinity was 4–5‰, and ammonium nitrogen concentrations were high (1.2–2.6 MPC). The maximum recorded concentration of ammonium nitrogen in the seawater during the observation period was 13.8 MPC, on June 9, 2023 at station 1, located 25 km from the mouth of the Dnieper Estuary at 5‰ salinity. Concentrations of ammonium nitrogen in seawater higher than the MPC (equal to 0.5 mg/L, a standard measure of dimethyl carbonate production) indicated that sewage wastewater and water from livestock farms had entered the Sea; ammonium is a form of mineral nitrogen that is readily utilized by micro- and macrophytes and can promote algal blooms. By the end of August, salinity levels had stabilized and concentrations of mineral and organic nitrogen substances and dissolved oxygen in the seawater returned to average seasonal levels.

Concentrations of phosphates and silicic acid, which are important biogenic substances, exceeded the average long-term values by 2–3 times, off the Odesa coast in June 2023, at 4‰ salinity, but maximum phosphate concentrations did not exceed the MPC. By August 2023, concentrations of phosphates and silicic acid, as well as concentrations of mineral and organic nitrogen substances and dissolved oxygen levels, had returned to average seasonal levels.

Biological toxicity test results

Seawater samples taken on June 9, 2023 in northern Odesa Bay (at station 2), three days after the Kakhovka Dam's release, used in controlled laboratory survival tests of the indicator species *Daphnia magna* resulted in moderately increased mortality (+27.8 ± 1.1% compared to control levels), which was lower than levels indicating acute lethal toxicity. However, on June 11, 2023, values of + 82.4 ± 2.4% exceeded the 50% toxicity threshold, indicating acute lethal toxicity levels. Values of + 74.6 ± 3.1% on June 13, 2023 also indicated high toxicity levels. On subsequent days, water quality toxicity levels fell below the established standards for toxicological quality; thus, the higher pollutant levels were relatively short in duration.

Biodiversity and community responses to the freshwater released from the Kakhovka Dam breakage, Study II *(adapted from Minicheva et al. 2023)* and Study III (fishes) *(adapted from Tkachenko et al 2025)*

Satellite chlorophyll-a observations, Study II

Satellite data tracked the spatial dynamics and temporal trends of a resultant algal "bloom" post-release of the Kakhovka Reservoir waters, based on the estimated concentration of chlorophyll-a. These showed the bloom's intensity and the density of phytoplankton in the coastal outflow in the NWBSR of the Dnieper River Estuary and in the Odesa region (Fig. 4). At the end of June 2023, chlorophyll-a levels reached + 170% above the annual average seasonal concentrations, peaking at + 280% in

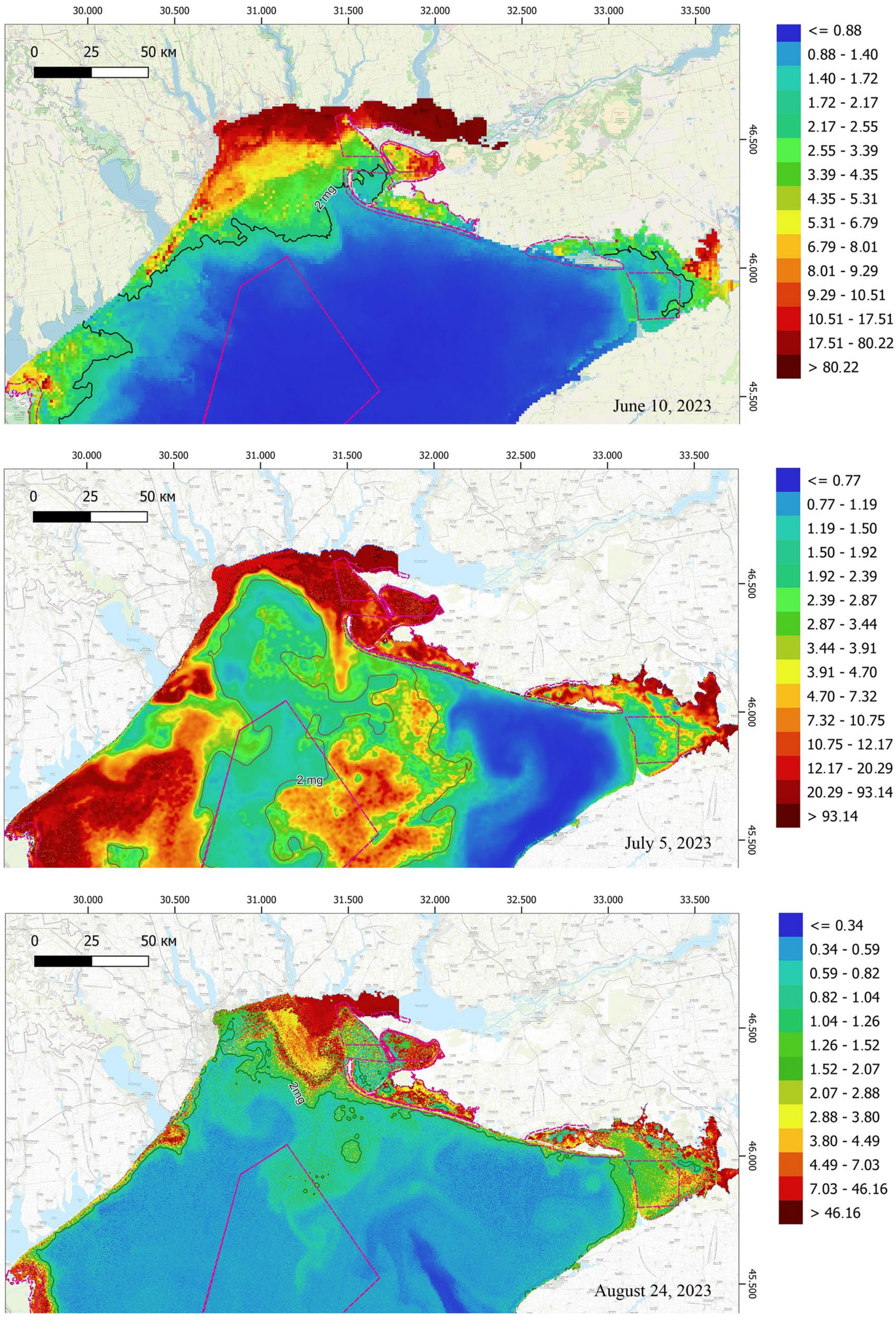

Fig. 4 Chlorophyll-a concentrations in the Northwestern Black Sea region in summer 2023 following the Kakhovka Dam's breakage on June 6, 2023 and water release (Study II; the original figure was designed by G. Minicheva and Y. Sokolov, who donated it for use here; this was modified by YK)

early July, after which mixing and blending spread the polluted water masses across most of the NWBS continental shelf. By the end of August 2023, chlorophyll-a levels had returned to their seasonal average values (see Fig. 4).

Phytoplankton responses, Study II

Two weeks after the Kakhovka Dam breakage, cyanobacteria (blue-green algae) levels peaked on June 18, 2023, reaching record bloom values of about + 1400% increase (Table 1). These increases involved + 2000% of the filamentous *Aphanizomenon flos-aquae* (Phylum Cyanobacteria, Family Aphanizomenonaceae), which is a widespread, nitrogen-fixing fresh–brackish water species that can release toxins that can accumulate in zooplankton and fishes, and + 70% of the filamentous benthic cyanobacteria freshwater *Jaaginema kisselevii* (Family Pseudanabaenaceae); both species are widespread in northern cold-temperate waters. Diatom increases peaked about a week after the disaster (June 11, 2023), by + 80% for *Skeletonema costatum* (Phylum Heterokontophyta, Family Skeletonemataceae)—a coastal marine, cosmopolitan-distributed and nutrient-rich centric species, which is consumed by crustacean larvae (see Kumar et al. 2023) and by + 50% for *Cylindrotheca closterium* (Family Bacillariaceae)—also a cosmopolitan-distributed marine, centric species. The released nutrients from the Dam fueled these increases. In July through August 20, 2023, phytoplankton composition and levels then returned to the previous average seasonal levels (Table 1).

Microzooplankton (< 200 µm) responses, Study II

There was a marked increase in heterotrophic flagellates in Odesa Bay, peaking on the 10th day (June 15) with numbers (1797 individuals (ind)/cm^3) increasing by + 300% from previous summers, and biomass (1667×10^6 mg/cm^3) increasing by + 122%, whose levels remained high for the next two weeks. The number of microzooplankton species increased by + 86%, including freshwater species that had not previously been observed in the NWBSR; species abundances and numbers then returned to normal in July and August.

Phytobenthos effects, Study II

13 types of macrophytes and 12 types of epiphytic microalgae were recorded, including species belonging to the phyla Bacillariophyta (10 species), Chlorophyta (6 species), and Rhodophyta (6 species). In June–August 2023, the benthos was dominated by the marine green algae species *Cladophora vagabunda* (Family Cladophoraceae), the red marine algae *Ceramium siliquosum* var. *elegans* (Family Ceramiaceae), the fresh–brackish water green algae *Ulva intestinalis* (Family Ulvaceae), and three marine benthic diatom species: *Cocconeis scutellum* var. *scutellum* (Family Cocconeidaceae), *Rhoicosphenia abbreviata* (Family Rhoicospheniaceae), and *Tabularia fasciculata* (Family Fragilariaceae).

Due to the phytoplankton bloom in June 2023, the macrophyte community was inhibited by light and available nutrient levels. The macrophyte community subsequently increased by + 83% above seasonal average levels at the end of July, since multicellular macrophytes have a longer developmental life cycle, much larger body sizes, and lower physiological activity than do phytoplankton (Zalumi 1967; Minicheva et al. 2018). Just prior to this, epiphytic microalgae peaked from June 29–July 15, 2023, increasing to + 50% levels above normal; this group occupies an intermediate position between phytoplankton and macrophytes in terms of response time to ecological changes and nutrient levels.

Zooplankton community effects, Study II

The zooplankton community declined slightly after the Kakhovka Dam's release to 78–99.5% of the annual average numbers and by 82–100% in biomass, compared to the monthly regional averages (Table 1). On one day alone (June 26, 2023) there was a significant zooplankton increase of + 457% in numbers and + 817% in biomass due to large numbers of the native Calanoida copepod complex *Acartia clausi* + *tons*a (Family Acartiidae) (58,900 individuals (ind)/m^3, 1332.5 mg/m^3) and the invasive cyclopoid copepod *Oithona davisae* (Order Cyclopoida, Family Oithonidae) (460 ind/m^3, 7.1 mg/m^3) (see Fig. 5). Another atypical species was the freshwater/brackish cladoceran crustacean *Podonevadne trigona* (Class Branchiopoda, Family Podonidae) (station 1 on June 1, 2023 with 27,400 ind/m^3, and in smaller numbers at station 4 from June 15 and later at 20–240 ind/m^3). Zebra mussel larvae also were recorded, which typically occur in fresh waters of the Dnieper River basin but not in marine waters (on June 11 at station 4). Species composition and levels returned to average seasonal values by mid-August 2023 (Table 1).

Macrozoobenthos response, Study II

Macroinvertebrate species that live attached to the substrate or are sedentary, and thus were subjected to direct effects of water conditions during the freshwater releases from the Kakhovka Dam, were monitored and assessed. These included 56 fouling macrozoobenthic taxa at depths of 0–5 m, which were dominated in numbers by Polychaeta (16 taxa), Mollusca (8), and Crustacea (26). The native mussel *Mytilaster lineatus* dominated in abundance from 0 to 3 m, whereas the introduced mussel *Mytilus galloprovincialis* had greater biomass representation. However, because salinity remained below

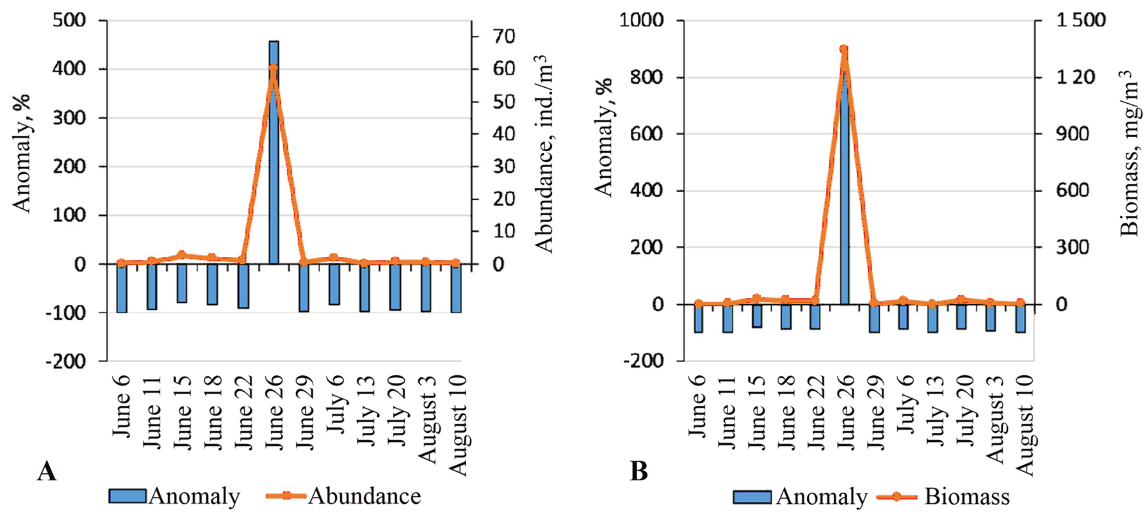

Fig. 5 Anomalies (measured as % difference from five-year seasonal average values) in zooplankton abundance **A** and zooplankton biomass **B** in the Northwestern Black Sea coastal waters at the Gulf of Odesa, Ukraine during summer 2023, after the Kakhovka Dam's breakage and freshwater release on June 6, 2023 (Study II;adapted from Minicheva et al. 2023; the original figure was designed by O. Bondarenko and R. Migas, who donated it for use here)

8‰ from June to mid-July at 0–3 m, mass mortality of *M. galloprovincialis* occurred (583 ± 115 ind/m^2; biomass 4089.5 ± 973.7 g/m^2). The freshwater release killed an estimated 39.6% of the *M. galloprovincialis* population, which predominantly were larger individuals (> 20 mm in length) that constituted a large proportion of the reproductive population. The total biomass of the dead mussel population (including all species) in this area of freshwater influx across the NWBSR (Fig. 1, lower left) was estimated at 3680.1 tons. Yet, such die-offs of *M. galloprovincialis* often occur in the region during periods of low oxygen and eutrophication (Zaitsev and Mamaev 1997). An increase in *M. lineatus* numbers was observed (from 72,952 ± 26,814 to 132,616 ± 30,552 ind/m^2), which is a more euryhaline and stress-resistant species.

In apparent response to the freshwater release and phytoplankton bloom, from June to mid-July, coinciding with their peak reproductive periods, numbers of small detritivores (including polychaetes) increased by 660% and numbers of small herbivores by 1400%. These increases lessened but persisted throughout this investigation period (Table 1); the zoobenthic community thus was slower to rebound from the salinity decrease, but exhibited longer-term changes.

Meiobenthos response, Study II

The sublittoral meiobenthic community, having body sizes 0.1–2.0 mm and located in the sediment to 1–5 m deep, was dominated by members of the following taxonomic groups: 56% Phylum Nematoda, 10% Order Harpacticoida (Class Copepoda), 10% young Bivalvia, and 8% Polychaeta. This community also contained species of Foraminifera, mites (Phylum Arthropoda, Class Arachnida, Family Halacarida), flatworms (Phylum Platyhelminthes, Class Turbellaria), mud dragons (Phylum Kinorycha), segmented worms (Phylum Annelida, Class Clitellata –formerly classified in the paraphyletic Oligochaeta), and *Amphibalanus* barnacles. Some of these increased in numbers from their seasonal averages by 503–1513% during the study period. By the end of August 2023, the relatively environmentally sensitive harpacticoids had increased in frequency, suggesting recovery from the pollutants released from the Dam.

Fish community response, Studies II and III

Prior to the Kakhovka Dam's construction, freshwater fishes often traveled into the NWBS with spring flood waters from the rivers and their estuaries (Tkachenko 2024a, 2024b). These included the common carp *Cyprinus carpio* (Family Cyprinidae), zander *Sander lucioperca* (Family Percidae), roach *Rutilus rutilus* (Family Cyprinidae), and Prussian carp, which were occasionally caught in Odesa Bay (whose salinity fluctuates from 5–6‰ to 17–18‰ seasonally) (Tkachenko 2024a, 2024b; Tkachenko et al. 2025). Two days after the flood, on June 8, 2023 in the Odesa NWBSR, dead common carp weighing 3–4 kg were observed, followed in subsequent days by roach, Prussian carp, and pumpkinseed sunfish (Minicheva et al. 2023). Very large numbers of dead freshwater fishes were washed into the NWBSR during this period, whose decay affected water quality and the food web (Krumenacker 2023; Minicheva et al. 2023).

In an interview on July 13, 2023, published in *Ukrainska Prava,* Mykola Solskyi, the Minister of Agrarian Policy and Food of Ukraine, stated that as a result from drainage of the Kakhovka Reservoir, 11,400 tons of fishes were lost, worth an estimated U.S. $267 M (Krumenacker 2023). The Kakhovka Reservoir previously served as a habitat to at least 43 fish species, 20 of which are commercially important (with annual catches up to 2600 tons). It was estimated that it would take at least 7–10 years to restore the lost fishery stocks (Krumenacker 2023).

In the before and after study of fish diversity and abundances in the Dnieper Estuary (Study III: Fig. 1 map, lower right) conducted by Tkachenko et al. (2025) and overviewed here, 25 fish species were collected following the Kakhovka Dam's breakage (from June 6 through August 16, 2023). Their occurrences and relative abundances were compared to 10 years of collection data made with the same sampling gear, methodology, investigators, and effort in the same locations (Fig. 6). Results indicated that three freshwater fish species increased in numbers in the two months following the Dam's breach (Fig. 6): rudd *Scardinius erythrophthalmus* (Family Cyprinidae), roach, and northern pike *Esox luceus* (Family Escodiae), all of which are widely distributed throughout European freshwaters and have broad ecological tolerances (Kottelat and Freyhof 2007). The formerly very abundant fresh–brackish water round goby and the monkey goby both decreased significantly (by about 10X) in comparison to their abundances before the Dam's breakage, from hundreds to thousands of individuals to tens in the net collections. Two freshwater fish species were newly recorded in this area after the Kakhovka Dam's water release: the environmentally tolerant freshwater weatherfish *Misgurnus fossilis* (Family Cobitidae) and the invasive Chinese sleeper, each represented by a single individual. The rare estuarine perch *Sander marinus* (Family Percidae) (see Haponski and Stepien (2013), for its evolutionary and ecological relationships) was not found in the collections after the Dam's destruction; this species had vanished from the region's watersheds until 2016, and is very sensitive to toxicants and lower salinity (Tkachenko et al. 2025).

In sampling the Dnieper Estuary locations during the two months following the Kakhovka Dam's breakage, marine fishes decreased in numbers, including the golden gray mullet *Chelon aurata* (Family Mugilidae) (Tkachenko et al. 2025), which is a plankton feeder that inhabits coastal and estuarine waters in the Mediterranean and Black seas, but is rare in freshwater (Kottelat and Freyhof 2007). Likewise, marine pelagic macroinvertebrates, encompassing jellyfishes, ctenophores, and shrimps, which were formerly common in the fish net catches throughout the previous 5–8 years of sampling, disappeared after June 6, 2023, attributed to their lower tolerances for freshwater conditions (Krumenacker 2023; Tkachenko et al. 2025).

If high freshwater flow continues, these community shifts that support freshwater species, likely will persist. Further studies have not been feasible after this to date, due to lack of access and dangerous conditions in the occupied territories of Ukraine during the ongoing War (and the 2024 death of Pavlo Tkachenko).

Habitat changes in the Dnieper Estuary, Study III

Extensive outflow of river water after the June 6, 2023 Kakhovka Dam's breakage washed away the marine macrophyte beds that were formerly abundant nearshore. After the flow stabilized (after June 12, 2023), the freshwater hornwort *C. demersum* took over, becoming markedly more abundant with 90–100% coverage from the coastline to ~ 15–25 m offshore and 70–80% to 200 m from the coast (a reach that previously had no macrophytes). Thus, the habitat vegetation significantly changed (Tkachenko et al. 2025). With the increased Dnieper River's freshwater outflow, the Dnieper Estuary region became much less saline, in contrast to the prior 5–8 years of increasing salinity (Tkachenko 2023).

The benthic macrophyte community before and during the War, Study IV

(new data and results by GGM)

Morphofunctional indicators of the benthic macrophyte (i.e., macrophytobenthos or seaweeds, encompassing macroalgae and seagrasses) community standardly have been used to assess the Ecological Status Class (ESC) of the Black Sea's coastal ecosystems (Minicheva 2013), in accordance with the requirements of the Marine Strategy Framework Directive (MSFD 2008) for the European Union (EU). These indicators are compared pre-War and during the War period through 2024. The first indicator, S/Wx, is the average ecological activity of the macrophytes, which is the intensity of biomass production by the macrophyte community (i.e., active growth). The value of this indicator decreases during favorable seasonal climatic conditions and also decreases with decreased anthropogenic load. Anthropogenic load declines when there is less disturbance to the ecosystem, such as fewer oil spills, pollutants, run-off, bottom trawling, or other fishing practices that negatively affect benthic primary productivity and plant habitats. All of these factors can markedly disturb or destroy the macrophyte community.

For example, during the first half of 2022 and the beginning of the War, weather conditions favored macrophyte

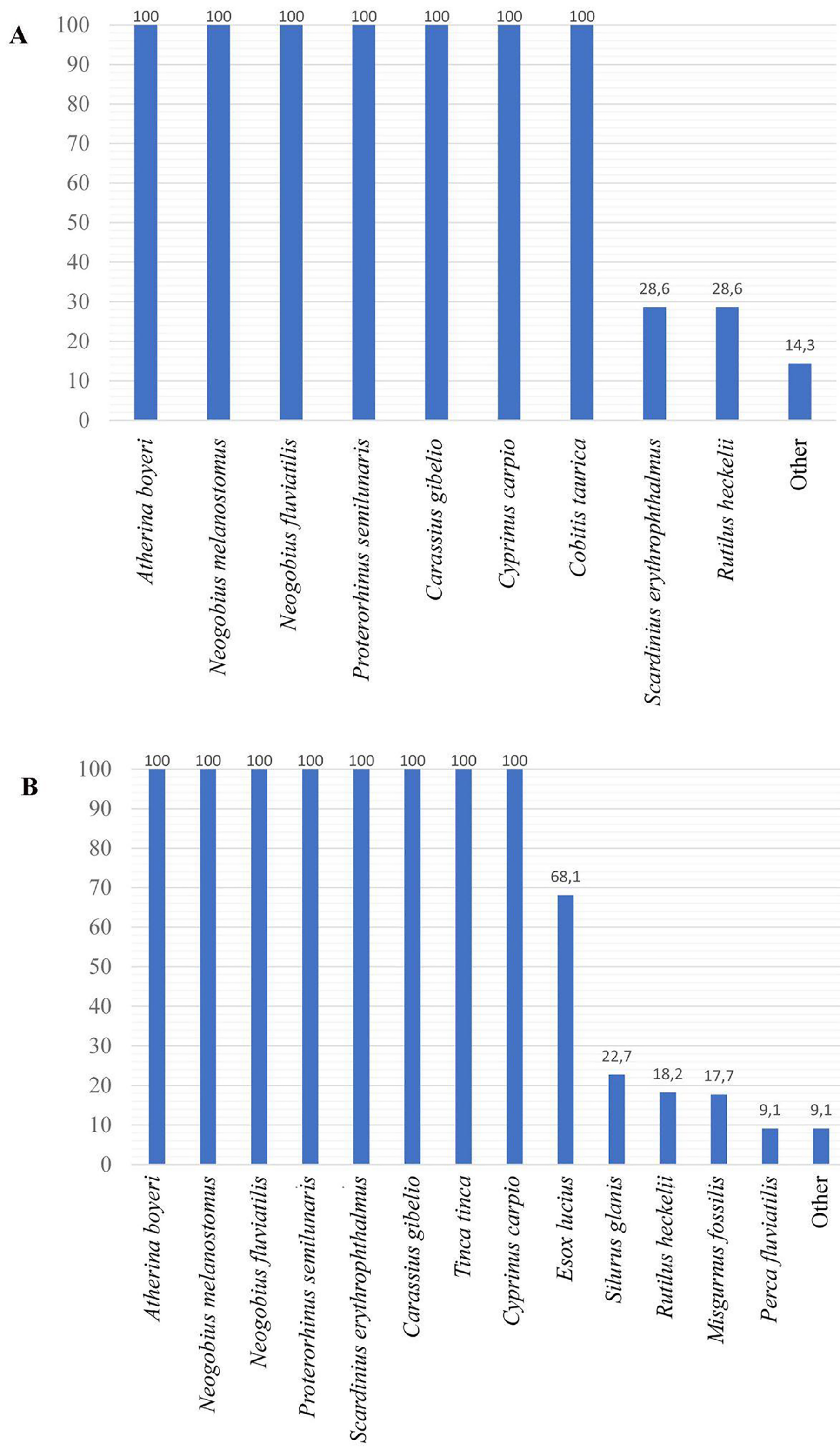

Fig. 6 Fishes obtained from sampling in summer 2023 in the Dnieper Estuary **A** before and **B** after the Kakhovka Dam breakage and water release (Study III, adapted from Tkachenko et al. (2025)). Bars denote the percent of individual net catches in which the species occurred. Fishes were collected using gill nets and fyke nets, and employing the same methodology, equipment, and locations over 10 years of sampling (Tkachenko 2024a, 2024b)

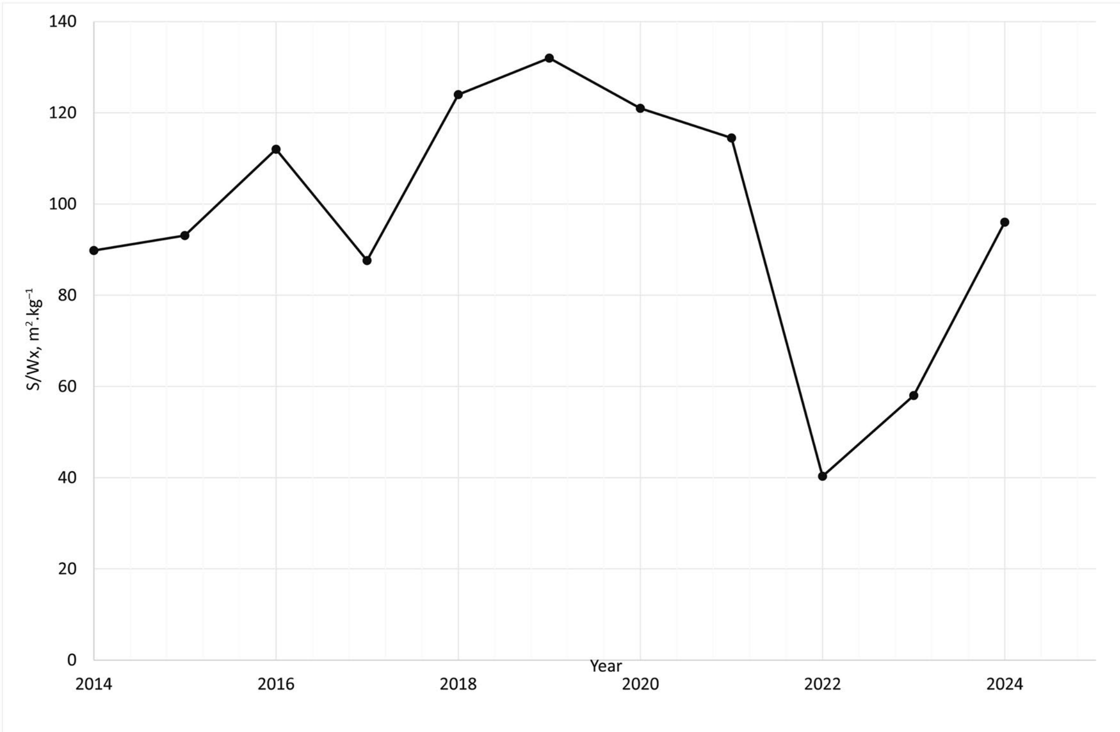

Fig. 7 Long-term dynamics of ecological activity of the benthic macrophytes community index (S/Wx) on the Odesa, Ukraine coast (Northwestern Black Sea), Study IV

primary productivity, due to low freshwater discharge from the rivers and moderate rainfall (i.e., salinity, nutrient, and light levels were stable) and low sea water temperatures. Thus, dissolved oxygen levels remained moderate and there were few surface phytoplankton blooms to block light and use up nutrients, which then supported benthic macrophyte photosynthesis and benthic community health. In addition, the anthropogenic load on the marine environment was low due to lack of fishing, benthic trawling, boat traffic, and beach tourism due to War prohibitions. These lower wartime anthropogenic pressures led to the overall improvement in the ecological health of the marine ecosystem and the benthic macrophyte community along the Odesa coast (Fig. 7). During the second half of 2022 and throughout 2023, climatic conditions became less favorable, and the recreational load on the Odesa coast also partially resumed. Accordingly, the indicator values began to increase again (see Fig. 7). The increase in 2023 was compounded by the Kakhovka Dam breakage, after which the indicator values have continued to increase.

Another morphofunctional indicator for macrophytes is the Surface Index (SI), which characterizes the intensity of the autotrophic process, using a classification scale of five ranking categories for the ESC (i.e., "High", "Good", "Moderate", "Poor", and "Bad"), meeting the requirements and standards of the Water Framework Directive (WFD 2000). The SI indicator values for the Odesa coast in the NWBS also reveal that favorable climatic conditions (water clarity, low temperatures, and stable nutrient levels) and decreased anthropogenic load led to an improvement in the ESC in 2022. In 2023 and 2024, the SI values began to increase due to greater phytoplankton blooms and their die-offs, and less light and nutrients consequently were available for the benthic macrophytes. Accordingly, the ESC categories also declined, from "High" to "Good" ecosystem health values (Fig. 8).

Overall, the levels of both indicators indicate some improved health of the benthic macrophyte community during the early War period (2022–2023), but indicator values have changed more recently (2024) to pre-War levels, attributed to increasing anthropogenic load. This may be due to cumulative longer-term habitat disturbances from the War (Figs. 7 and 8). IMB researchers plan to continue to monitor these trends.

Changes in invasive aquatic species during the War

Influxes of invasive species into the NWBSR have continued during the War, and some may have accelerated due to opening up of freshwater and estuarine niches following the Kakhovka Dam's destruction (see Tkachenko et al. 2025). For example, the range of the invasive

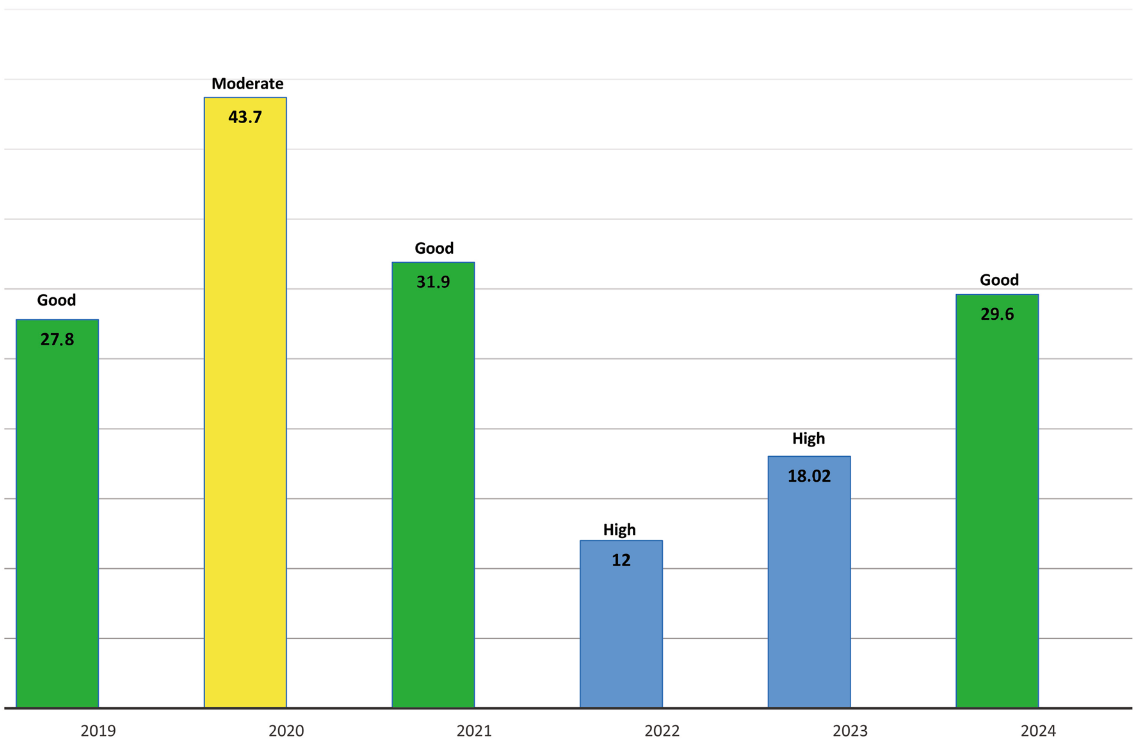

Fig. 8 Changes in Ecological Status Class (ESC) using morphological indicators for the benthic macrophyte community along the Odesa Northwestern Black Sea coast in the pre-War (2019–2022) and War period (2022–2024), based on Surface Index (SI) units and the five ESC categories (here ranging in rank from "Moderate" to "High"; Study IV)

Chinese sleeper fish has spread in the Dnieper Estuary, after the freshwater deluge in June 2023, likely due to flooding and releases from aquaculture ponds in the region (Tkachenko et al. 2025). In contrast, numbers and occurrences of the invasive Prussian carp have remained consistent in the Dnieper Estuary (Tkachenko et al. 2025). The Prussian carp has been widely introduced and is known for its ability to thrive in marginal-quality habitats that are less suitable for most native freshwater species; i.e., the Prussian carp is more tolerant of hypoxia, environmental pollution, moderate salinity, turbidity, and high levels of eutrophication (summarized by Ruppert et al. 2017). The Korean rockfish *Sebastes schlegelii* (Family Scorpaenidae) is a new fish invader, discovered in the Sukhyi Lyman Estuary near Chornomorsk (46.2952°N, 30.6481°E) in 2023 (Kvach and Khutornoi 2025).

Among invertebrates, the Atlantic blue crab from the coast of North America, which is a well-established invasive species in the Mediterranean Sea (Mancinelli et al. 2017; Sabelli 2023), has recently appeared in the NWBS off Odesa, increasing its range. Notably, a gravid female of about 20 cm was collected in June 2024 by an angler off Chornomorsk, suggesting an established population (YK, personal observation).

Further habitat damage during the War

War activity around Kherson (46.6354°N, 32.6169°E), especially around the bridge over the Dnieper River, has been among the most severe to date (Krumenacker 2023). Since February 2022, access to the marine components of two Protected Areas (PAs) have been lost: the Chornomorsky Black Sea Biosphere Reserve and the National Natural Park "Biloberezhia Sviatoslava", both located in southern Kherson (Conflict and Environment Observatory (CEO) (2023). Situated about 45 km southwest of Kherson, the Black Sea Biosphere Reserve contains shallow coastal lakes and estuaries, inland wetlands, dunes, halophytic coastal steppes, and forests, and was recognized as a UNESCO Biosphere Reserve in 1984. Russian forces have occupied the Black Sea Biosphere Reserve since the start of their full-scale invasion. Extensive long-lasting fires around the Black Sea Biosphere Reserve and the National Natural Park have been observed from satellites, numbering some 67 fires in 2022 and 141 in 2023, which burned 6300 hectares of land; as a result, extensive reaches of unique habitats were destroyed (Krumenacker 2023). The damage to these habitats and their species, and their recovery potential, will be important to document and assess.

Additionally, a very valuable, unique and very fragile steppe ecosystem exists on the Crimean Peninsula, which is important to European biodiversity; it appears unknown what the effects of the Russia–Ukraine War have been on it. Notably, Shypotilova et al. (2021) has raised concerns about uncontrolled fishing, discharge of wastewater from the coastal cities of Crimea, significant pollution due to the activities of the Black Sea Fleet and operations of drilling rigs, and destruction of the unique seabed communities in the Karkinitsky and Kalamitsky bays (see Fig. 3A) with pollution from chemical industry near the borders of the Marine Protected Areas (MPAs).

Long-term consequences throughout the Black Sea marine ecosystem are projected to include secondary pollution from toxins released from benthic sediments, and bioaccumulation of oil products and other toxins (Vyshnevskyi et al. 2023), with corresponding influence on biodiversity. The overall long-term effects of the habitat changes on component species compositions and diversity, as well as their persistence remain to be discerned.

The response and potential long-term resilience of these Black Sea area species and ecosystems will be critically important to document and analyze, including habitat and distributional data, accurate species inventories, and specimen voucher preservation. These data are vitally important to understand and recover from this international conflict and other anthropogenic events.

Records, museum preservations, and specimens for comparisons

Historical samples, data, and records will provide essential comparative data towards analyzing the after-effects of the Russia–Ukraine War and to aid ecological restoration in these valuable and unique habitats. For example, contributions to the Global Biodiversity Information Facility (GBIF 2025) provide access to global species, organizing information, including barcode DNA sequence data where available; additional input of data from Ukraine will be extremely valuable. GBIF's aim is to promote connections and assign persistent species identifiers, and archive data that are discoverable and resolvable using controlled vocabularies, data standards, ontologies, and to provide open access for all. In addition, the Ocean Biological Information System (OBIS 2025), endorses a joint strategy and action plan for marine biodiversity data, with GBIF and OBIS both being built on the same meta(data) model (Heberling et al. 2021).

The Schmalhausen Institute of Zoology of the National Academy of Sciences of Ukraine in Kiev collects, catalogs, studies, and maintains scientific specimen collections documenting biodiversity, encompassing its Departments of Invertebrate Fauna and Systematics, Evolutionary and Genetic Systematics, Fauna and Taxonomy of Vertebrates, Evolutionary Morphology and Wildlife Monitoring and Conservation (including the Lab of Population Ecology), and others (http://www.izan.kiev.ua). The specimen collections of the National University of Luhansk, located in the Russian-occupied Donbas region were relocated in 2014 to become part of the collection of the Natural History Museum of the National Academy of Sciences of Ukraine in Kiev. The State Museum of Nature of the V. N. Karazin Kharkiv National University in Kharkiv, in northeast Ukraine, which is Ukraine's second largest city, houses major scientific and marine zoological collections (https://karazin.ua/en/kultura/muzei-prirodi/). The Museum remains open to students and scientists, despite Kharkiv being under attacks throughout the War and at present.

The present and possible biodiversity future

The Dnieper–Bug river system flood from the Kakhovka Dam breach and massive flooding on June 6, 2023, and the ecosystem's rapid desalination likely moved along restoring the ecosystem's former salinity and flow parameters towards conditions that existed prior to the construction of the Dam and its Reservoir during the 1960s. During the short period of water release by the broken Dam, marine/brackish water fishes in the Dnieper Estuary region disappeared or decreased in numbers, and representation of the freshwater fauna increased. The core of the Dnieper Estuary fish fauna has comprised freshwater species, which has remained stable before and after the disaster. During the decade prior to June 2023, marine fauna (including fishes, jellyfishes, ctenophores, and shrimps) had appeared and increased in numbers in the Estuary due to increasing salinity conditions resulting from decreased freshwater inflow and prevailing southwestern winds in the prior 5–8 years (Tkachenko 2023). After the Dam's destruction, the source of the increased prevalence of freshwater fishes, including newly documented species, was the Lower Dnieper River and the Kakhovka Reservoir.

Overall, the ecosystems of the Dnieper–Bug Estuary region thus have exhibited plasticity and adaptability, with fish deaths and declines that occurred after the Kakhovka Dam breakage exerting short-term effects. The marine–estuarine nearshore NWBS community near the port area of Odesa also has exhibited ecological recovery and resilience following the initial fish and mussel community deaths. It is possible that the further spread of the invasive Chinese sleeper was due to the flood that followed. The freshwater, estuarine, and marine macrophyte communities also have shown restored growth along the coastlines. Thus, the ecological paradox of the situation is the positive effect of the Kakhovka Dam release disaster on the Dnieper–Bug Estuary ecosystem, in favoring the original freshwater community, and the positive effects of reduced anthropogenic stressors on the marine, estuarine and freshwater biota overall.

Conclusions

As a result of military actions commencing in 2022, both negative impacts (oil spills, consequences of shelling, explosions, fires) and positive impacts (cease of all types of peaceful anthropogenic loads—shipping, fishing, recreation, construction, hydraulic engineering) of the Russia–Ukraine War have affected the overall biodiversity and habitats of the Black Sea region. Apparent ecological releases to date, stemming from prohibitions on commercial fishing and closed tourism, have allowed fisheries, beaches, and coastal and nearshore species and their habitats to rebound. The greatest ecological damage to date has been the Kakhovka Dam's destruction on June 6, 2023, which resulted in extensive downstream flooding with freshwater and pollutant releases, killing many riverine, estuarine, and marine Black Sea populations and inundating nearshore habitats.

Based on sampling and analyses conducted by IMB scientists, we conclude that many of those biological effects appear to have been temporary so far, with habitats and species replenishing, and some reverting to their historic biota characteristic of lower salinity regimes. However, significant long-term habitat destruction, disturbances, and pollutant damages remain and are continuing with the ongoing War. Since much of the northern Black Sea biota is dominated by species that evolved in conditions favoring broad salinity, temperature, and oxygen tolerances, this ecosystem appears pre-adapted for ecological recovery and persistence, which may equate to environmental resilience during and after the War.

The marine, estuarine, and freshwater communities of the northern Black Sea overall display ecological persistence and adaptability that are likely to resonate towards community continuity despite the ongoing perturbations of the War, climate change, global transportation, and invasive species—meriting worldwide conservation focus and cooperation. The growing synergy among globally accessible biodiversity databases, remote sensing, artificial intelligence, and museum preservation resources, and knowledge of DNA sequences and genomic adaptations, promise enhanced ability to document such effects towards biodiversity conservation and preservation.

Abbreviations

MPA	Marine Protected Area
NWBS	Northwestern Black Sea
NWBSR	Northwestern Black Sea Region
PA	Protected Area

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Author contributions
Both first authors (YK and CAS) made equal and substantial contributions to the conception and design of the work, and the writing and analysis interpretations presented in this paper. CAS drafted the narrative and corrected the manuscript. GGM led the Dam release study (Study II) and the macrophyte study (Study IV) and the oil spill analysis (Study I) that are summarized here, and made comments and corrections. PT led the fish Dam release study co-authored by YK (Study III), and PT tragically is deceased.

Authors Information
CAS and YK have been collaborating since 2002 on ecology of marine, estuarine, and freshwater macroinvertebrates and fishes, including invasive and native species in Ukraine and throughout the Ponto-Caspian region. CAS is a Research Associate with the Smithsonian's National Museum of Natural History and is an elected fellow of the American Association for the Advancement of Science. YK is a research scientist at the Institute of Marine Biology (IMB), National Academy of Sciences (NAS) of Ukraine in Odesa. GGM is the Director of the IMB, NAS, a marine biologist and expert on macrophytes and nearshore ecology. PT was a scientific researcher at the Black Sea Biosphere Reserve, NAS, located in Gola Pristan (this area has been occupied by Russian forces during the War). PT studied the fish communities of the Lower Dnieper River and adjacent parts of the Black Sea over the last 25 years. This was his final fish survey (he had to evacuate the region, and then died in April 2024).

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Availability of data and materials
All relevant data are provided in the paper. Please see Minicheva et al. (2023), minicheva@ukr.net for any additional data about the Dam release study summarized here and Tkachenko et al. (2025) for the fish collection summary.

Declarations

Ethics approval and consent to participate
Not applicable. Fish collections are summarized here from standard collection procedures and permits under Tkachenko et al. (2025), held by the Institute of Marine Biology (IMB), National Academy of Sciences of Ukraine (NASU).

Consent for publication
Not applicable.

Competing interests
The authors declare there are no competing interests.

Author details
[1]Institute of Marine Biology, National Academy of Sciences of Ukraine, Odesa 65048, Ukraine. [2]Department of Vertebrate Zoology Research Associate, Smithsonian Institution, National Museum of Natural History, Washington, DC 20013-7012, USA. [3]Black Sea Biosphere Reserve, National Academy of Sciences of Ukraine, Lermontova Street, 1, Gola Pristan 75600, Ukraine.

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References

Alexandrov B, Minicheva G, Zaitsev Y (2017) Black Sea network of Marine Protected Areas. In: Goriup DP (ed) Management of Marine Protected Areas. John Wiley & Sons, Ltd., Hoboken, NJ, USA. pp 227–246. https://doi.org/10.1002/9781119075806.ch12

Arbačiauskas K, Lesutienė J, Gasiūnaitė ZR (2013) Feeding strategies and elemental composition in Ponto-Caspian peracaridans from contrasting environments: can stoichiometric plasticity promote invasion success? Freshw Biol 58:1052–1068. https://doi.org/10.1111/fwb.12108

Bacela K, Konopacka A (2005) The life history of *Pontogammarus robustoides*, an alien amphipod species in Polish waters. J Crustacean Biol 25(2):190–195. https://doi.org/10.1651/C-2519

Bakan G, Buyukgungor H (2000) The Black Sea. Mar Pollut Bull 41(1–6):24–43. https://doi.org/10.1016/S0025-326X(00)00100-4

Briggs JC (1974) Marine Zoogeography. McGraw-Hill Co., New York, NY, 475 pp

Brockmann C, Doerffer R, Peters M, Kerstin S, Embacher S, Ruescas A (2016) Evolution of the C2RCC neural network for Sentinel 2 and 3 for the retrieval of ocean colour products in normal and extreme optically complex waters. Living Planet Symposium. In: Ouwehand L (ed) Proceedings of the conference held 9–13 May 2016 in Prague, Czech Republic. ESA-SP Volume 740, p 54. https://ui.adsabs.harvard.edu/abs/2016ESASP.740E..54B/abstract. Accessed 14 Jan 2025

Brown JE, Stepien CA (2008) Ancient divisions, recent expansions: phylogeography and population genetics of the round goby *Apollonia melanostoma*. Mol Ecol 17(11):2598–2615. https://doi.org/10.1111/j.1365-294X.2008.03777.x

Brown JE, Stepien CA (2010) Population genetic history of the dreissenid mussel invasion: expansion patterns across North America. Biol Invasions 12(11):3687–3710. https://doi.org/10.1007/s10530-010-9763-2

CMS (2023) Copernicus Marine Service—CMEMS (Copernicus Marine Environment Monitoring Service). https://marine.copernicus.eu/. Accessed 14 Jan 2025

Conflict and Environment Observatory (2023) Ukraine conflict environmental briefing: The coastal and marineenvironment. Ceobs.org

Copilaş-Ciocianu D, Sidorov D (2022) Taxonomic, ecological and morphological diversity of Ponto-Caspian gammaroidean amphipods: a review. Org Divers Evol 22:285–315

Cristescu MEA, Witt JDS, Grigorovich IA, Hebert PDN, MacIsaac HJ (2004) Dispersal of the Ponto-Caspian amphipod *Echinogammarus ischnus*: invasion waves from the Pleistocene to the present. Heredity 92:197–203. https://doi.org/10.1038/sj.hdy.6800395

Dobrzycka-Krahel A, Stepien CA, Nuc Z (2023) Neocosmopolitan distributions of invertebrate aquatic invasive species due to euryhaline geographic history and human-mediated dispersal: Ponto-Caspian versus other geographic origins. Ecol Proc 12:2. https://doi.org/10.1186/s13717-022-00412-x

Dudliv I, Kvach Y, Tkachenko MY, Nazaruk K, Ondračková M (2024) Comparative analysis of parasite load on recently established invasive pumpkinseed *Lepomis gibbosus* (Actinopterygii: Centrarchidae) in Europe. Acta Parasitol 69(1):819–830. https://doi.org/10.1007/s11686-024-00794-2

Fleminger A, Hulsemann K (1987) Geographical variation in *Calanus helgolandicus* s.l. (Copepoda, Calanoida) and evidence of recent speciation of the Black Sea population. Biol Oceanogr 5(1):43–81. https://doi.org/10.1080/01965581.1987.10749505

Gagnon P, St-Hilaire-Gravel LV, Himmelman JH, Johnson LE (2006) Organismal defenses versus environmentally mediated protection from herbivores: unraveling the puzzling case of *Desmarestia viridis* (Phaeophyta). J Exp Mar Biol Ecol 334(1):10–19. https://doi.org/10.1016/j.jembe.2006.01.012

García-García D, Vigo MI, Trottini M, Vargas-Alemañy JA, Sayol J-M (2022) Hydrological cycle of the Mediterranean-Black Sea system. Clim Dyn 59:1919–1938. https://doi.org/10.1007/s00382-022-06188-2

GBIF (2025) Global Biodiversity Information Facility. https://www.gbif.org/. Accessed 14 Jan 2025

Geina K (2019) The biological status of commercial flocks of carp of the Dnieper-Bug Estuary system. Ecol Sci 2:108–111. https://doi.org/10.32846/2306-9716-2019-1-24-2-21. (in Ukrainian with English summary)

Gleick P, Vyshnevskyi V, Shevchuk S (2023) Rivers and water systems as weapons and casualties of the Russia–Ukraine War. Earth's Future 11:e2023EF003910. https://doi.org/10.1029/2023EF003910

Gomoiu M-T, Alexandrov B, Shadrin N, Zaitsev Y (2002) The Black Sea—a recipient, donor and transit area for invasive species. In: Leppäkoski E, Gollasch S, Olenin S (eds) Invasive Aquatic Species of Europe: Distribution, Impacts and Management. Springer, Dordrecht. pp 341–350. https://doi.org/10.1007/978-94-015-9956-6_35

Grabowska J, Kvach Y, Rewicz T, Pupins M, Kutsokon I, Dykyy I, Antal L, Zięba G, Rakauskas V, Trichkova T, Čeirāns A, Grabowski M (2020) First insights into the molecular population structure and origins of the invasive Chinese sleeper, *Perccottus glenii*, in Europe. NeoBiota 57:87–107. https://doi.org/10.3897/neobiota.57.48958

Guiry MD, Guiry GM (2024) AlgaeBase. World-wide electronic publication, University of Galway. https://www.algaebase.org. Accessed 14 Jan 2025

Haponski AE, Stepien CA (2013) Phylogenetic and biogeographical relationships of the *Sander* pikeperches (Perciformes: Percidae): patterns across North America and Eurasia. Biol J Linn Soc 110(1):156–179

Heberling JM, Miller JT, Noesgaard D, Schigel D (2021) Data integration enables global biodiversity synthesis. PNAS 118(6):e2018093118. https://doi.org/10.1073/pnas.2018093118

Hryhorczuk D, Levy BS, Prodanchuk M et al (2024) The environmental health impacts of Russia's War on Ukraine. J Occup Med Toxicol 19:1. https://doi.org/10.1186/s12995-023-00398-y

Hulak BS, Leonchyk YY, Chashchyn OK (2022) The main biological parameters of Rapa whelk *Rapana venosa* population in the North-Western section of the Black Sea. Hydrobiol J 58(3):29–45. https://doi.org/10.1615/HydrobJ.v58.i3.30

Ilyin YP (2023) Average condition and seasonal variability of the structure and dynamics of transitional waters in the Dnieper-Bug Estuary region. Ukr Hydromet J 32:63–79. https://doi.org/10.31481/uhmj.32.2023.05

IUCN (2025b) The European Red List. https://www.iucnredlist.org/regions/european-red-list. Accessed 14 Jan 2025

IUCN (2025a) Invasive Species Specialist Group. https://www.iucn.org/our-union/commissions/group/iucn-ssc-invasive-species-specialist-group. Accessed 14 Jan 2025

Kajiyama T, D'Alimonte D, Zibordi G (2018) Algorithms merging for the determination of chlorophyll-a concentration in the Black Sea. IEEE Geosci Remote Sens Lett 16(5):677–681. https://doi.org/10.1109/LGRS.2018.2883539

Karamanlidis AA, Dendrinos P, Fernandez de Larrinoa P, Kıraç CO, Nicolaou H, Pires R (2023) *Monachus monachus*. IUCN Red List of Threatened Species. 2023: e.T13653A238637039. https://doi.org/10.2305/IUCN.UK.2023-1.RLTS.T13653A238637039.en

Karsiotis SI, Brown JE, Pierce LR, Stepien CA (2012) Salinity tolerance of the invasive round goby: experimental implications for seawater ballast exchange and spread to North American estuaries. J Great Lakes Res 38:121–128. https://doi.org/10.1016/j.jglr.2011.12.010

Khutornoi S, Son MO, Kvach Y (2023) First record of two fish species (Actinopterygii) in the Sukhyi Lyman, northwestern Black Sea, Ukraine. Acta Ichthyol Piscat 53:157–162. https://doi.org/10.3897/aiep.53.111525

Kideys AE (2002) Fall and rise of the Black Sea ecosystem. Science 297(5586):1482–1482. https://doi.org/10.1126/science.1073002

Kostylev EF, Tkachenko FP, Tretiak IP (2010) Establishment of "Zernov's *Phyllophora* field" marine reserve: protection and restoration of a unique ecosystem. Ocean Coast Manag 53(5–6):203–208. https://doi.org/10.1016/j.ocecoaman.2010.04.010.

Kottelat M, Freyhof J (2007) Handbook of European Freshwater Fishes. Publications Kottelat, Cornol and Freyhof, Berlin, 646 pp

Krumenacker T (2023) Ukrainian dam collapse triggers 'Ecological disaster'. Scientific American. June 9, 2023. https://www.scientificamerican.com/article/ukrainian-dam-collapse-triggers-ecological-disaster/#:~:text=Flooding%20from%20the%20draining%20reservoir,the%20Dnipro%20Delta%20are%20threatened Accessed 14 Jan 2025

Kumar NA, Sridhar S, Jayappriyan KR, Raja R (2023) Chapter 33—Applications of microalgae in aquaculture feed. In: Jacob-Lopes E, Queiroz MA, Maroneze MM, Queiroz Zepka L (Eds) Handbook of Food and Feed from Microalgae. Academic Press, pp 421–433. https://doi.org/10.1016/B978-0-323-99196-4.00011-5

Kvach Y, Kutsokon Y (2017) The non-indigenous fishes in the fauna of Ukraine: a potentia ad actum. BioInvasions Rec 6(3):269–279. https://doi.org/10.3391/bir.2017.6.3.13

Kvach Y, Kutsokon Y, Stepien CA, Markovych M (2016) Role of the invasive Chinese sleeper *Perccottus glenii* Cybowi 1877 (Actinopterygii: Odeontobutidae) in the distribution of fish parasites in Europe: new data and a review. Biologia 71(8):941–951. https://doi.org/10.1515/biolog-2016-0112

Kvach Y, Kutsokon Y, Demchenko V, Yuryshynets V, Kudryashov S, Abramiuk I (2022) Post-invasion spread of Chinese sleeper (*Perccottus glenii*) in the

Lower Danube drainage (Budjak region of Ukraine). BioInvasions Rec 11(2):547–559. https://doi.org/10.3391/bir.2022.11.2.27
Kvach Y, Khutornoi S (2025) The Korean rockfish, *Sebastes schlegelii* Hilgendorf, 1880 (Actinopterygii: Scorpaeniformes: Sebastidae)—a new component in the North-Western Black Sea coastal fish fauna. BioInvasions Rec 14 [accepted for publication]
Mancinelli G, Chainho P, Cilenti L, Falco S, Kapiris K, Katselis G, Ribeiro F (2017) The Atlantic blue crab *Callinectes sapidus* in southern European coastal waters: distribution, impact and prospective invasion management strategies. Mar Pollut Bull 119(1):5–11. https://doi.org/10.1016/j.marpolbul.2017.02.050
Mandych AF (ed) (1995) Enclosed Seas and Large Lakes of Eastern Europe and Middle Asia. SPB Academic Publishing, Amsterdam, p 270
Manné S, Poulet N, Dembski S (2013) Colonisation of the Rhine basin by non-native gobiids: an update of the situation in France. Knowl Manag Aquat Ecosyst 411:02. https://doi.org/10.1051/kmae/2013069
Marciano K (2023) How the War in Ukraine takes a devastating toll on Nature. Audubon Magazine, Fall 2023. https://www.audubon.org/news/how-war-ukraine-takes-devastating-toll-nature. Accessed 14 Jan 2025
Minicheva G (2013) Use of the macrophytes' morphofunctional parameters to assess ecological status class in accordance with the EU WFD. Mar Ecol J 12(3):5–21. https://emblasproject.org/wp-content/uploads/2013/12/Minicheva_WFD.pdf
Minicheva G (2015) Finding of alien brown macroalgae *Chorda tomentosa* Lyngby. in the Ukrainian Black Sea coast. J Black Sea Medit Environ 21(2):227–231
Minicheva GG, Yeremenko TI (1993) Algologicheskie nakhodka v severo-zapadnoy chasti Chernogo morya [Algological findings in the North-Western Black Sea]. Algologia 3(4):83–87 (in Russian)
Minicheva G, Sokolov E (2024) Application of space technologies to assess the ecological state and consequences of military operations on the marine ecosystems of Ukraine. In: Fedorov O (ed) Space research in Ukraine, 2022–2024. PH "Akademperiodyka", Kyiv. pp 79–85. https://doi.org/10.15407/akademperiodyka.507.172
Minicheva GG, Zotov AB, Kosenko MN (2003) Methodical recommendations on the morpho-functional indexes define for unicellular and multicellular forms of aquatic vegetation. Printed in accordance with the resolution of the Scientific Council of the OB IBSS from the June 26, 2003, protocol No. 8. CNTEPI ONYUA, Odessa, 40 pp. https://www.researchgate.net/publication/325650981
Minicheva GG, Bolshakov VN, Zotov AB (2010) The response of autotrophic communities of the northwestern Black Sea to the variability of climatic factors. J Environ Protect Ecol 11(3):1046–1054
Minicheva GG, Bolshakov VN, Kalashnik ES, Zotov AB, Marinets AV (2018) Assessment of the reactions of the Black Sea ecosystem's algae communities to influence of climatic factors. Algologia 28(2):121–135. https://doi.org/10.15407/alg28.02.121
Minicheva GG, Bondarenko OS, Bogatoya YI, Bushuiev SG, Garkusha OP, Dyatlov SY, Kalashnik ES, Koshelev OV, Kudrenko SA, Kulakova II, Marinets AV, Migas RV, Martynyuk MO, Nikonova SY, Rybalko OA, Synyogub IO, Sokolov YV, Stadnichenko SV, Khutornoi SO, Vinogradov OK, Kvach YV, Demchenko VO, Son MO (2023) Reaction of the marine ecosystem to the consequences of destruction of the Kakhovka Reservoir dam. Mar Ecol J (1–2):52–68. https://doi.org/10.47143/1684-1557/2023.1-2.6 (in Ukrainian with English summary)
Movchan YV (2011) Ryby Ukrainy [Fish of Ukraine], Zoloti Vorota, Kyiv, Ukraine 444 p. (in Ukrainian)
MSFD (2008) EU Marine Strategy Framework Directive (MSFD, 2008/56/EC). Directive 2008/56/EC of the European Parliament and of the Council establishing a framework for community action in the field of marine environmental policy, 17 June 2008. https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX%3A02008L0056-20170607. Accessed 14 Jan 2025
Nations Online Project (2024) Map of the Black Sea. https://www.nationsonline.org/oneworld/map/Black-Sea-political-map.htm. Accessed 14 Jan 2025
Neilson ME, Stepien CA (2009a) Escape from the Ponto-Caspian: evolution and biogeography of the neogobiin species flock (Gobiidae: Teleostei). Mol Phylogenet Evol 52:84–102. https://doi.org/10.1016/j.ympev.2008.12.023
Neilson ME, Stepien CA (2009b) Evolution and phylogeography of the tubenose goby genus *Proterorhinus* (Gobiidae: Teleostei): evidence for new cryptic species. Biol J Linn Soc 96(3):664–684. https://doi.org/10.1111/j.1095-8312.2008.01135.x
OBIS (2025) Ocean Bioinformatic Information System (OBIS). Intergovernmental Oceanographic Commission (IOC). 12 Dec. 2024. https://manual.obis.org and https://www.gbif.us/post/2024/gbif-obis-joint-action-plan/. Accessed 14 Jan 2025
OSG (2024) Open Geospatial Consortium. https://www.ogc.org. Accessed 14 Jan 2025
Osikowski A, Hofman S, Georgiev D, Kalcheva S, Falniowski A (2016) Aquatic snails *Ecrobia maritima* (Milaschewitsch, 916) and *E. ventrosa* (Montagu, 803) (Caenogastropoda: Hydrobiidae) in the East Mediterranean and Black Sea. Ann Zool 66(3):477–486. https://doi.org/10.3161/00034541ANZ2016.66.3.012
Paidere J, Brakovska A (2022) The Ponto-Caspian and native amphipod life history in the Daugava River, Latvia. Oceanol Hydrobiol Stud 51:268–282. https://doi.org/10.26881/oahs-2022.3.03
Pereira P, Zhao W, Symochko L, Inacio M, Bogunovic I, Barcelo D (2022) The Russian-Ukrainian armed conflict impact will push back the sustainable development goals. Geogr Sustain 3(3):277–287. https://doi.org/10.1016/j.geosus.2022.09.003
Popov SV, Ilyina LB, Paramonova NP et al (2004) Lithological-Paleogeographic Maps of Paratethys. Courer Forschungsinstitut Senckenberg
Poulos SE (2023) Water masses of the Mediterranean Sea and Black Sea: an overview. Water 15(18):3194. https://doi.org/10.3390/w15183194
Ramsar (1971) Ramsar Convention on Wetlands. Convention on wetlands of international importance, especially as waterfowl habitat. 2.2.1971. https://rsis.ramsar.org/about. Accessed 14 Jan 2025
Reid DF, Orlova MI (2002) Geological and evolutionary underpinnings for the success of Ponto-Caspian species invasions in the Baltic Sea and North American Great Lakes. Can J Fish Aquat Sci 59:1144–1158. https://doi.org/10.1139/f02-099
Revkov NK, Boltacheva NA, Timofeev VA, Bondarev IP, Bondare LV (2018) Macrozoobenthos of the Zernov's *Phyllophora* Field, Northwestern Black Sea: species richness, quantitative representation and long-term variations. Nat Conserv Res 3(4):32–43. https://doi.org/10.24189/ncr.2018.045
Rewicz T, Wattier R, Grabowski M, Rigaud T, Bącela-Spychalska K (2015) Out of the Black Sea: phylogeography of the invasive killer shrimp *Dikerogammarus villosus* across Europe. PLoS ONE 10(2):e0118121. https://doi.org/10.1371/journal.pone.0118121
Roche KF, Janač M, Jurajda P (2013) A review of gobiid expansion along the Danube-Rhine corridor—geopolitical change as a driver for invasion. Knowl Manag Aquat Ecosyst 411:01. https://doi.org/10.1051/kmae/2013066
Ruppert JLW, Docherty C, Neufeld K, Hamilton K, MacPherson L, Poesch MS (2017) Native freshwater species get out of the way: Prussian carp (*Carassius gibelio*) impacts both fish and benthic invertebrate communities in North America. R Soc Open Sci 4:170400. https://doi.org/10.1098/rsos.170400
Sabelli C (2023) What scientists know about the blue crab invasion. Nature Italy. https://www.thebdri.com/ecs2023abstractbook.pdf. Accessed 14 Jan 2025
Sentinel Application Platform (SNAP, version 9.0) software package. https://step.esa.int/main/download/snap-download/. Accessed 14 Jan 2025
Shypotilova O, Kozhanov A, Lohinova L, Lohinov O (2021) The problem of the Black Sea pollution in Odessa region of Ukraine. IOP Conf Ser Earth Environ Sci 915:012008. https://doi.org/10.1088/1755-1315/915/1/012008
Šidagytė E, Arbačiauskas K (2016) Resistance to low oxygen in the Ponto-Caspian amphipod *Pontogammarus robustoides* varies among lentic habitats of its northern invaded range. Limnologica 61:7–13. https://doi.org/10.1016/j.limno.2016.09.001
Slastenenko E (1956) Karadeniz havzasi baliklari [The fishes of the Black Sea basin]. E.B.K. Yayini, Istanbul, 711 pp. (in Turkish)
Sousa R, da Silva JP, Douda K, Mammola S (2022) The cost of war for biodiversity: a potential ecocide in Ukraine. Front Ecol Environ 20(7):394–396. https://doi.org/10.1002/fee.2548

Stanev EV, Peneva EL (2001) Regional sea level response to global climatic change: Black Sea examples. Global Planet Change 32(1):33–47. https://doi.org/10.1016/S0921-8181(01)00148-5

Stepien CA, Brown JE, Neilson ME, Tumeo MA (2005) Genetic diversity of invasive species in the Great Lakes versus their Eurasian source populations: insights for risk analysis. Risk Anal 25(4):1043–1060. https://doi.org/10.1111/j.1539-6924.2005.00655.x

Stepien CA, Grigorovich IA, Gray MA, Sullivan TJ, Yerga-Woolwine S, Kalacyi G (2013) Evolutionary, biogeographic, and population genetic relationships of dreissenid mussels, with revision of component taxa. In: Nalepa TF, Schloesser DW. Quagga and Zebra Mussels: Biology, Impacts, and Control. 2nd Ed. CRC Press, Boca Raton, FL. pp 403–444

Stevens T, Mee L, Friedrich J, Aleynik D, Minicheva G (2019) Partial recovery of macro-epibenthic assemblages on the North-West Shelf of the Black Sea. Front Mar Sci 6:474. https://doi.org/10.3389/fmars.2019.00474

Thiel R, Schulze S, Hempel M, Husemann M (2017) Most northerly record of the bighead goby *Ponticola kessleri* (Günther, 1861) in the Elbe River, Germany. Bioinvasions Rec 6(1):73–78. https://doi.org/10.3391/bir.2017.6.1.12

Tkachenko PV (2023) Adaptation of biological cycles of fishes in the Tendra, Yahorlyk bays and adjacent waters of the Black Sea to environmental changes related to recent climate Changes. Hydrobiol J 59(5):64–79. https://doi.org/10.1615/HydrobJ.v59.i5.40

Tkachenko PV (2024a) Marine fish species in the Dnieper Estuary in the modern period. Hydrobiol J 60(2):39–56. https://doi.org/10.1615/HydrobJ.v60.i2.30

Tkachenko PV (2024b) Fish species of the Red Data Book of Ukraine in the Dnieper-Bug Estuary and the Lower Dnieper in the Modern Period. Hydrobiol J 60(5):35–46. https://doi.org/10.1615/HydrobJ.v60.i5.40

Tkachenko PV, Markautsan O, Kvach Y (2025) Relocation of fish populations to estuaries and bays of the North-Western section of the Black sea as a consequence of technogeneous disasters and natural processes in 2023. Hydrobiol J 61(2):30–46. https://doi.org/10.1615/HydrobJ.v61.i2.30

Tuchkovenko YS, Kushnir DV, Ovcharuk VA, Sokolov AV, Komorin VN (2023) Characteristics of Black Sea dispersion of freshened and polluted transitional waters from the Dnipro-Bug Estuary after destruction of the Kakhovka Reservoir dam. Ukr Hydromet J 32:95–114. https://doi.org/10.31481/uhmj.32.2023.07

Verlatiy DB, Mezhzherin SV, Fedorenko LV (2009) Species structure and catches of anadromous and freshwater fishes of Lower Dnieper estuarine system: dynamics in the 21th century and comparison with the Lower Danube. Vestnik Zoologii 43(3):231–244 (in Russian with English summary)

Vinogradov AK, Bogatova YI., Synegub IA (2018) Ecology of marine ports of the Black and Azov Sea Basin. Cham, Springer International Publishing. 412 pp. https://doi.org/10.1007/978-3-319-63062-5

Vishnyakova K, Tonay AM, Povov D, et al. (2023) An unusually high number of cetacean strandings in the Black Sea, 2022—is it the consequence of war? In: 34th European Cetacean Society Conference: Abstract book. Poster 144. https://www.thebdri.com/ecs2023abstractbook.pdf. Accessed 14 Jan. 2025

Vorobyova LV, Kulakova II, Synyogub IA, Polyschuk LN, Nesterova DA, Bondarenko AS, Snigirova AA, Rybalko AA, Kudrenko SA, Portyanko VV, Migas RV, Uzun YY, Olephir IV (2017) Odessa region of the Black Sea: hydrobiology of pelagic and benthic areas. Astroprint, Odessa, 321 pp. (in Russian with English summary)

Vučković N, Pozojević I, Urbanič G, Mihaljević Z (2021) New evidence supporting upstream pathways of *Hypania invalida* (Grube, 1860) invasion. BioInvasions Rec 10(3):589–597. https://doi.org/10.3391/bir.2021.10.3.08

Vyshnevskyi V, Shevchuk S, Komorin V, Oleynik Y, Gleick P (2023) The destruction of the Kakhovka Dam and its consequences. Water Int 48(5):1–17. https://doi.org/10.1080/02508060.2023.2247679

WFD (2000) EU Water Framework Directive (WFD, 2000/60/EC). Directive 2000/60/EC of the European Parliament and of the Council establishing a framework for the community action in the field of water policy, 23 October 2000. https://eur-lex.europa.eu/eli/dir/2000/60/oj Accessed 14 Jan 2025

WoRMS (2024) World Register of Marine Species. https://www.marinespecies.org/. Accessed 14 Jan 2025

Yankova M, Pavlov D, Ivanova P, Karpova E, Boltachev A, Öztürk B, Bat L, Oral M, Mgeladze M (2014) Marine fishes in the Black Sea: recent conservation status. Medit Mar Sci 15(2):366–379. https://doi.org/10.12681/MMS.700

Zaitsev YP, Mamaev V (1997) Marine biological diversity in the Black Sea: a study of change and decline. Black Sea Environmental Series (3). United Nations Publications, New York, NY. 208 p. https://fishermenassociation.wordpress.com/wp-content/uploads/2014/10/biological-diversity-in-the-black-sea-1.pdf Accessed 14 Jan 2025

Zaitsev YP, Alexandrov BG, Berlinsky N, Zenetos A (2002) The Black Sea: an oxygen-poor sea. In: Europe's biodiversity—biogeographical regions and seas. Environmental issue report EEA (European Environment Agency), Copenhagen. http://reports.eea.eu.int/report_2002_0524_154909/en

Zaitsev YP, Aleksandrov BG, Minicheva GG (2006) Severo-Zapadnaya chast Chernogo morya: biologiya i ekologiya [North-Western Black Sea: Biology and Ecology]. Naukova Dumka, Kiev, 701 pp. (in Russian)

Zalumi SG (1967) Ichthyofauna changes in the Low Dnieper River and the Dnieper-Bug Estuary in connection with hydroconstruction. Vestnik Zoologii 3:66–69 (in Russian with English summary)

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