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Climate change in the "vulnerable" Eastern Mediterranean and adjacent areas: A literature review of ecological impacts and threats

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ABSTRACT

The Mediterranean Sea (MS) represents a complex system that acts as a convergence zone for various biogeographical influences stemming from both temperate and tropical oceanic bodies. Its intricate topography has promoted speciation and adaptation, leading to the development of distinctive and varied marine sites. The MS has a greater total alkalinity than the open ocean, which allows it to absorb a larger amount of human-induced CO₂ per unit of surface area, suggesting an increased threat of acidification. The Eastern Mediterranean (EM) region has been identified as a critical climate change (CC) hotspot; by the end of the 21st century, it is anticipated that heatwaves in the EM will occur more than seven times as often and last more than three times as long. Here, we provide an extensive literature review on the CC-induced impacts and threats on biota throughout EM and adjacent areas, supporting potential mitigation actions.

The key elements contributing to the impacts and threats posed by CC in the region are: ocean warming (OW), ocean acidification (OA), and the synergistic effects of OW and OA. Additional factors encompass the combination of: i) OW and marine heatwaves (MHWs), ii) OW and non-indigenous species (NIS), iii) OW and desertification, and iv) OW and water circulation. However, the primary factor causing biodiversity decline, not just in the EM region but throughout the entire MS, seems to be the introduction of NIS, which is further worsened by OW. The primary route through the Suez Canal (SC) and its continuous expansions have sparked worry about the rising propagule pressure. There is a growing consensus that if these environmental risks are not comprehended and mitigated, a significant portion of the Mediterranean ecosystem may face severe threats to its integrity.

Ultimately, the initiative of dumping brine waste into the SC, acting as a high salinity barrier that would reduce the transfer of new species carried by the currents, is likely a practical and attractive first step towards mitigation. We suggest that this action should be embraced not only by other countries but also by international environmental organizations and agencies, through a variety of strategies, including financial support. This initiative, along with other measures aimed at alleviating the impacts of invasions on biodiversity, ecosystem services, and health, is an essential next step in the process of mitigation.

Abbreviations			(continu	(continued)			
				CC	Climate change	MS	Mediterranean Sea
Ag	Silver	MMEs	Mass mortality events	Cd	Cadmium	MTC	Mean temperature of catch
			(continued on next column)				(continued on next page)

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(continued)

CC	O_2	Carbon dioxide	NIS	Non-indigenous species
Cι	1	Copper	OA	Ocean acidification
EC	250	Half maximal effective concentration	OW	Ocean warming
EN	M	Eastern Mediterranean	pCO_2	Partial pressure of carbon dioxide
H	gS	Mercury sulfide	PP	Primary production
H	Ws	Heatwaves	RS	Red Sea
IA	S	Invasive alien species	SC	Suez Canal
M	F	Mediterranean fisheries	SST	Sea surface temperature
M	HWs	Marine heatwaves	Zn	Zinc

1. Introduction

The primary physical changes in the marine system, due to climate change (CC) involve ocean warming (OW), (Barnett et al., 2001; Hollowed and Sundby, 2014), the rising fluctuation in climate resulting in an uptick of extreme occurrences (Rahmstorf and Coumou, 2011; Frölicher et al., 2018), and alterations in sea level, thermal stratification, water circulation, and upwelling (Harley et al., 2006; Schmittner, 2005; Wang et al., 2015). In addition, the combination of OW and changes in ocean currents work together to decrease oxygen levels in the deep sea (Shepherd et al., 2017) and release carbon dioxide, which leads to ocean acidification (OA). These processes can impact the environment in two ways: directly, such as when the sea temperature surpasses a species' physiological limits, and indirectly, such as changes in habitat accessibility, species interrelations, and production rates (Worm and Lotze, 2021). Other consequences involve nutrient enrichment, habitat ruin, species incursions, and impact on the fishing industry (Lotze and Worm, 2002; Hoegh-Guldberg et al., 2007; Murray et al., 2015).

In general, researchers are gradually gaining a better understanding of how changes in biodiversity are linked to temperature fluctuations, both over time (Mannion et al., 2014) and across different geographical areas (Tittensor et al., 2010; Worm and Tittensor, 2018). The primary focus of studies examining the effects of CC on ecosystems, both on land and in the ocean, has been on individual species (e.g. Parmesan and Yohe, 2003; Parmesan, 2006). Lately, researchers have been investigating community metrics, like structure and variety of species, linking to fluctuations and alterations in climate (Menéndez et al., 2006; Hiddink and Ter Hofstede, 2008; Cheung et al., 2009; Jones and Cheung, 2015; Pinsky et al., 2013). The impacts of recent climate variations overlap with other existing stressors that have already affected biodiversity (Harnik et al., 2012), making it challenging to attribute observed changes to a specific factor. The reduction of biodiversity has been suggested to potentially limit the variety of biotic responses to CC, which could also diminish adaptive capability (Elmqvist et al., 2003; Schindler

The OW and OA, along with reductions in dissolved oxygen levels and alterations in primary productivity, are leading to an unparalleled global shift in the dispersal of marine species. Recently, it has been demonstrated that many communities and locations have distinctly reacted to the continuing upsurge in OW, evidenced by a 54 % rise in warm-water species (tropicalization) and an 18 % reduction in coldwater species (deborealization) (Chust et al., 2024); partially enclosed Seas, like the Mediterranean Sea (MS), seem to be particularly vulnerable to OW, facing some of the highest rates of warming and a significant decline in biodiversity.

The history of MS is complex, making it a meeting point for various biogeographical influences from both temperate and tropical oceanic masses; its intricate topography, with a complex coastline, sub-basins, straits, islands, and circulation patterns, has led to speciation and adaptation, creating unique and diverse seascapes and biogenic assemblages at both global and local scales (Coll et al., 2010). The area it covers in the global ocean is only 0.8 %, and its volume is merely 0.3 %,

but it is home to an impressive variety of life, with 4–18 % of the planet's marine species found there, depending on the specific group of organisms being considered (Bianchi et al., 2012). The statement above recognizes the MS as a 'miniature ocean' (Lejeusne et al., 2010), compressing the interface connecting pressures and receptors (habitats and species), therefore providing a relevant platform to evaluate the ecological impacts of CC on biological diversity and appraise possible adaptation and mitigation approaches (Cramer et al., 2018; Aurelle et al., 2022).

The overall alkalinity of the MS is higher than that of the open ocean due to water exchange with the Atlantic and Black Sea, along with river inputs and calcium carbonate sedimentation (Schneider et al., 2007). Its elevated total alkalinity, combined with its strong overturning circulation and comparatively high temperatures, means it has a greater ability to absorb human-caused CO2, suggesting that its potential pH decrease is higher than that of the nearby Atlantic Ocean (Hassoun et al., 2022), thus leading to a heightened risk of acidification. Nonetheless, the amount of man-made CO2 taken in by the MS is still not known (Palmiéri et al., 2015). Touratier and Govet (2011) indicate that in 2001, even the most profound depths of the MS showed signs of acidification with pH levels dropping from 0.14 to 0.05 since the start of the industrial age. Moreover, the water transferred through the Otranto Strait in 1995 showed a substantial decline in pH compared to the normal levels. (Krasakopoulou et al., 2011). Nevertheless, associated time series are inadequate in the MS (Hassoun et al., 2022) and particularly in the Eastern Mediterranean (EM) (Frangoulis et al., 2024).

While OA is expected to be more severe in the semi-enclosed and densely populated MS, there are still major gaps in our knowledge about its trends and the resulting biological effects. (Hassoun et al., 2022). Nevertheless, Pallacks et al. (2023) report that higher OA in the MS resulted in decreased sizes and weights in foraminifera across the basin due to changes in calcification; they predict that continued increases in OA will cause further declines in biogenic calcification in the MS.

The EM and Middle East regions have been identified as key focal points for climate change (Zittis et al., 2022). Human-induced emissions, including CO₂, are increasing at a rapid pace, surpassing those of the European Union, whereas over the past few decades, the EM has been warming nearly two times more rapidly than the average observed globally, and notably faster than other regions (Zittis et al., 2022). Throughout the remainder of the century, the same authors anticipate a temperature increase of over 5 °C, accompanied by a significant rise in the intensity and duration of heatwaves (HWs). Wedler et al. (2023) suggest that by the end of the 21st century, HWs in the EM are anticipated to increase in frequency by sevenfold and extend in duration by threefold

Marine heatwaves (MHWs) are globally increasing their frequency over the past 20 years, along with their duration, intensity, and geographical extent (IPCC, 2022), and this increase is expected to become significantly more pronounced in the MS (Darmaraki et al., 2019, 2024). Ibrahim et al. (2021) analyzed the spatial variability and patterns of MHWs in the EM from 1982 to 2020, focusing on their main characteristics; they found that during the past two decades, their average frequency rose by 40 %, while their average duration increased by 15 %. Over the past ten years, the southern Aegean Sea has experienced a minimum MHW duration of 10 days, whereas off the coast of Israel, it has reached over 27 days (Ibrahim et al., 2021).

The warming trend is especially noticeable even in the Red Sea (RS). Since 1994, a clear increase in temperature has been recorded, which has become more pronounced since 2016. This temperature rise coincided with a higher frequency and overall number of MHWdays in the region. Over the past forty years (1982–2021), the basin has experienced 78 MHW events, totaling 1016 days of high temperature (Hamdeno et al., 2024). It should be highlighted that 46 % of the occurrences and 58 % of the days with high temperatures happened in the past ten years. Finally, the connection between 35 climate factors, atmospheric circumstances, and the presence of MHWs in the RS was emphasized

(Hamdeno et al., 2024).

Concerning bioinvasions in the EM (and finally throughout MS), the Suez Canal (SC) is a border between EM and RS; there is no other pathway for non-indigenous species (NIS) around the world that has consistently generated such large numbers as long in one specific area (Galil, 2023).

Here, we provide an extensive literature review on the CC-induced impacts and threats on marine life concerning, directly or indirectly, the EM and adjacent areas. The structure has been heavily based on the available information. The included sections encompass benthic communities, plankton communities, marine fisheries, NIS, marine birds, and metal toxicity. We aim to identify the most vulnerable issues in this system and ultimately locate potential mitigation actions.

2. Impact and threats on ecosystems, biodiversity, and community structure

2.1. Benthic communities

2.1.1. Habitat alteration and biodiversity shifts

Subtidal canopy-forming macroalgal communities, mainly formed by species of the genera Cystoseira, Ericaria, and Gongolaria (Orellana et al., 2019), as well as the genus Sargassum, constitute dominant Mediterranean euphotic rocky habitats. These habitat-forming perennial macroalgae represent the highest level of Mediterranean rocky reef complexity, provide shelter and nursery (Pinna et al., 2020) and thus establish and sustain complex organismal communities. However, diverse anthropogenic pressures in the Mediterranean throughout the late 20th century, including water quality decrease, habitat destruction, and trophic cascades, led to the degradation of macroalgal assemblages (Sala et al., 1998; Soltan et al., 2001; Thibaut et al., 2005). OW, combined with the increased frequency and force of MHWs in the past two decades, further increased pressure on the already degraded canopy-formers (Verdura et al., 2021) and intensified grazing by non-indigenous herbivores (e.g. Siganus luridus and S. rivulatus) (Tsiamis et al., 2013; Salomidi et al., 2016; Nikolaou et al., 2023).

Ongoing degradation has resulted in the complete removal of canopy-forming macroalgae along broad extents of coastline in the EM and the Levantine, creating extensive areas where the marine forest has been replaced by algal turf or reef barren (Tsiamis et al., 2013; Salomidi et al., 2016; Sala et al., 2011) with remarkably lower biodiversity (Pinna et al., 2020). Consequently, the current ecological status of shallow sublittoral reef communities (down to 15 m depth) over the extent of the Aegean Sea was recently assessed as 'bad' (Savin et al., 2023), leading to a significant impoverishment of coastal habitats in terms of primary productivity, biomass, and biodiversity, with a forecasted cascade effect to ecosystem services (Bevilacqua et al., 2021). This is expected to escalate by OW, extreme events, and the progression of newly introduced herbivorous species, such as the long-spined sea urchin *Diadema setosum* which shows alarming expansion since 2018 (Zirler et al., 2023).

A significant impediment to the assessment of current ecological status and, consequently, any effective restorative action in Mediterranean benthic habitats, is the lack of baseline reference studies. Biodiversity shifts are not systematically quantified, therefore leading to a 'sliding baseline syndrome' (Gatti et al., 2015), where an already degraded state can be recognized as a reference, thus lowering the ecological standards of evaluation. Notably, Bianchi et al. (2014) assessed the biodiversity of shallow (down to 10 m) habitats at Kos island (SE Aegean Sea) over a 30-year timespan (1981-2013). Striking differences were documented: 30 species were found in 1981 but not again in 2013 ('losses'), 38 were found exclusively in 2013 ('gains'), 16 increased their abundance ('winners'), eight got scarcer ('losers'), and only 28 underwent little or no change. Remarkably, the percent proportion of native thermophilic species almost doubled, while the establishment of NIS and loss of natives implied a dramatic species turnover of more than 60 %. Similar habitat and biodiversity shifts are documented in later studies, combining historical data and current observations over greater depth zones (down to 50 m) and time spans, reaching 70 years (Gatti et al., 2015; Bianchi et al., 2019), consistently identifying the tipping point of change during the abrupt climate shift of the 1990s

Albano et al. (2021) assessed the diversity loss on the shelf around Israel, the warmest area in the MS. They compared present molluscan diversity against historical death assemblages, finding that only 12 % and 5 % of historically native species remained on shallow subtidal soft and hard substrates, respectively. So far, this represents the most significant loss of regional diversity recorded in the marine system. In contrast, intertidal assemblages, which are more resilient to climatic fluctuations, alongside those in the cooler mesophotic zone, retained approximately 50 % of their historical diversity. Notably about 60 % of the shallow subtidal native species did not attain reproductive maturity, indicating that the shallow shelf acted as a demographic sink.

One of the most vulnerable marine habitats to CC is coastal lagoons (Newton et al., 2014), as they are directly affected by OW, reduced precipitation, and the resulting droughts and desertification, growing occurrence and force of tempests, and sea level rise (Taylor et al., 2021); all these might disrupt the fragile equilibrium of these habitats, resulting in regime shifts and anoxic episodes (Derolez et al., 2020).

2.1.2. Marine heatwaves driving mass mortality events

Mass mortality events (MMEs) are incidents where large numbers of organisms are eradicated along a specific area within a limited time. In the marine realm, mass mortalities of inconspicuous, short-lived, or economically unimportant organisms, often go unnoticed. On the other hand, reports of MMEs of economically relevant or emblematic organisms, often perceived as catastrophic events, e.g. the massive die-off of commercial sponges in the Caribbean Sea in the 1940s (Smith, 1941), or the recurrent bleaching of coral reefs in temperate regimes (Hughes et al., 2017).

In the MS, the first mass mortality incident reported in the scientific literature was the so-called sponge disease in 1986 with a devastating impact on commercial bath sponge stocks (mainly *Spongia officinalis* and *Hippospongia communis*) in the Aegean Sea and the Tunisian plateau (Pronzato, 1999). Regional sponge populations showed signs of recovery only after 1988 in the Aegean Sea (Voultsiadou et al., 2011), while in the Western Mediterranean, the impact of the event was less pronounced (Gaino et al., 1992).

Several small-to moderate-scale episodes of mass mortality were reported in the north-western Mediterranean basin during the 1990s, affecting different groups of sessile benthic invertebrates, such as anthozoans, sponges, bivalves and ascidians (Cerrano et al., 2000). Then, two MMEs of unprecedented scale followed in 1999 and 2003 (Pérez et al., 2000; Garrabou et al., 2009), extending over thousands of kilometers from the central Ligurian Sea to the Catalan coast and the Balearic Islands. Both events occurred in late summer to late autumn and were the first MMEs in the MS to be positively associated with MHWs. Gorgonian anthozoans were most affected by these events, mainly Eunicella singularis, E. cavolini, Paramuricea clavata, the precious Mediterranean red coral Corallium rubrum, as well as the scleractinian Cladocora caespitosa. Keratose sponges (S. officinalis, H. communis, Scalarispongia scalaris, Ircinia spp.) were also broadly affected, with partial or total necrosis.

Rivetti et al. (2014) provide a concrete link between temperature anomalies and mass mortality incidents in the MS, while Garrabou et al. (2022) document an acceleration of the ecological impact of MHWs in the last half of the 2010s along hundreds of kilometers of coastline and down to a depth of 45 m, affecting 50 marine taxa across eight phyla and directly linked with exceptional thermal conditions. These persistent trends suggest the establishment of the MHW/MME synergy as a tenacious feature within the Mediterranean ecoregion that is expected to shape future biodiversity patterns.

While temperature anomalies undoubtedly drive mass mortalities,

the precise mechanisms causing the death of the organisms remain largely unknown. The prolongation of summer conditions imposes energy constraints to benthic organisms through limitations to food availability, resulting in considerable biomass loss and partial necrosis (Coma et al., 2009). The resulting physiological stress can render the affected organisms more susceptible to opportunistic thermotolerant or thermo-dependent microorganisms. For example, the introduced pathogen Vibrio corallilyticus was indicated experimentally as the major factor responsible for the mortality of the cnidarian Paramuricea clavata during the 2003 MME (Bally and Garrabou, 2007). The native fan mussel Pinna nobilis has suffered a recent devastating epidemic effect from 2016 on, which brought it in the brink of extinction (Kersting et al., 2019). Mortality started at the Spanish coast and the Balearic Islands and spread eastwards in the next three years, causing mortality rates higher than 90 %, (Katsanevakis et al., 2022). The expansive spread of event was facilitated by water circulation patterns (Cabanellas-Reboredo et al., 2019), implying a pathogenic causative agent. The newly described haplosporidian parasite Haplosporidium pinnae appeared to be responsible (Tiscar et al., 2022), but additional experimental studies have indicated synergies with other opportunistic microorganisms such as Vibrio mediterranei and showed activation of pathogenicity in elevated temperatures above 25 °C (Prado et al., 2020). Similarly, Yeruham et al. (2015) found massive mortalities of the sea urchin Paracentrotus lividus in the Israeli coastline when temperatures exceeded 30.5 °C, suggesting that raised seawater temperatures may be the primary reason for the vanishing of the formerly abundant native species, thus indicating a distributional range shrinkage in the region.

The ecological consequences of MMEs are not confined to strict biodiversity loss defined as the reduction in abundance (or extinction) of particular taxa. Since most of the affected organisms are key species and habitat formers, their removal induces considerable repercussions for the architecture and functionality of benthic ecosystems, such as the highly productive Mediterranean coralligenous communities (Gómez-Gras et al., 2021) and other Marine Animal Forests (Rossi et al., 2022). Loss of ecological functions and habitat degradation can pose significant impacts on ecosystem services to local and global societies and economies (Smith et al., 2021).

2.1.3. Corals

Investigating the effects of the MHWs recorded from 2016 to 2022, on shallow assemblages of the habitat-creating Mediterranean octocoral *Paramurice clavata*, Rovira et al. (2024) report that the years during which mortality rates rose dramatically were the same years that experienced intense MHWs; they anticipate that the ability of this species to endure may not be sustained to support these populations as they confront the upcoming OW and MHWs.

Based on eight years of *in situ* data, the reaction of the two Mediterranean scleractinian corals *Cladocora caespitosa* and *Astroides calycularis* to projected OW and MHWs was examined (Carbonne et al., 2024). Certain colonies of *C. caespitosa* experienced significant bleaching while colonies of *A. calycularis* showed signs of necrosis. Rescue through various processes was noted for both species, indicating that both corals might withstand heat stress and can bounce back from the physiological challenges posed by MHWs.

Sani et al. (2024), examining how the simultaneous rise in OA and OW control the rate of tissue renewal in three Mediterranean scleractinian coral species, each exhibiting distinct trophic and growth patterns, detect a reduction in regenerative ability as temperature and acidification increased, along with noted variations among species; they propose that rising seawater temperatures and acidification may collectively impede coral regeneration after injury, potentially limiting the ability of corals to recover from bodily disruption anticipated under CC scenarios.

The dispersal patterns of symbiotic scleractinian corals are controlled, in part, by access to light, since the energy needs of the host are partly fulfilled through the transfer of photosynthetic products.

Goodbody-Gringley et al. (2024), analyzing the characteristics of both the host and its endosymbiotic organisms found on *Madracis pharensis* corals in Haifa Bay (Israel), confirm that these corals can modify various physiological characteristics of both the host and the symbiont based on the access to light; they emphasize their ability to shift towards a mainly heterotrophic diet when light levels and/or symbiont populations become insufficient for adequate photosynthesis, hence enhancing their adaptability against CC.

Mesophotic zones are believed to serve as possible safe havens from CC for gorgonian populations in MS, providing optimism for the reseeding of the harmed populations inhabiting shallow waters. The adaptability and responses of the yellow gorgonian *E. cavolini* were tested through a spectrum of environmental conditions by conducting mutual transplants between shallow (20m) and mesophotic (70m) areas (Beauvieux et al., 2024). It has been shown that yellow gorgonians found in mesophotic environments display higher adaptability when moved to shallower waters than shallow gorgonians do when relocated to the mesophotic location, indicating that *E. cavolini* could show physiological adaptability in reaction to forthcoming CC, facilitating natural settlement from mesophotic groups.

Shlesinger et al. (2024) report the presence of a vibrant and flourishing population of the exotic soft coral, *Dendronephthya hemprichi*, in the altering MS. The sudden occurrence of a large population near the Israeli coastline indicates a fast northward expansion from the northern RS. The rapid and extensive colonization of artificial structures by this species prompts important inquiries regarding its potential to transform benthic community dynamics and establish new marine animal habitats in the MS, highlighting the possible long-term ecological consequences. These results add to the wider conversation about the tropicalization of temperate and subtropical areas, emphasizing the importance of adjusting conservation approaches that recognize and comprehend new ecosystem configurations amidst continuous local and global transformations.

In general, the CC consequences on corals have been apparent since 2007, marked by coral bleaching and significant coral loss, occurring due to the exposure of reef flats from extreme low tides in the southern Egyptian RS (Tesfamichael and Pauly, 2016). Comparable tendencies have been recorded in the coral reefs of Saudi Arabia, where rising water temperatures (Baker et al., 2004) have led to reduced coral growth (Cantin et al., 2010), a decrease in large corals (Riegl et al., 2012), and widespread bleaching incidents (Kotb et al., 2008; Furby et al., 2013). Furthermore, unexpected surges in starfish populations have caused considerable damage to the coral reefs throughout the RS (Wilkinson, 2008). It has been proposed (Eladawy et al., 2022) that the northern RS will likely not reach the anticipated bleaching threshold (32 °C) prior to the conclusion of the 21st century; as a result, coral reefs in this region could potentially be among the last to survive in the battle against CC.

Globally, coral reefs are increasingly suffering from coral disease, which has been connected to human activities such as overfishing, excessive nutrient use, and heat stress. (Harvell et al., 2007). Aeby et al. (2021) performed disease assessments at 22 reefs across three RS areas, documenting 20 diseases that disturbed 16 coral taxa; even though the occurrence of the disease could not be linked either to coral cover or the duration of weeks with higher temperatures, they predict a rise in the occurrence of coral disease as a result of the elevated frequency and intensity of OW.

Cai et al. (2024) investigated the spatial and temporal distributions of 15 element concentrations in nine sediment cores from coral reefs to analyze the impact of OW and industrialization on the coral reefs of the Eastern RS. They note higher trace element levels in coral reefs experiencing significant bleaching, confirming earlier findings suggesting that trace elements could lower corals' resistance to thermal stress in warming conditions.

2.1.4. Impact and threats on life traits of organisms

CC-induced changes in the ocean chemistry can cause severe

sublethal effects which may affect future populations and the communities' composition. More specifically, disruption of the organism's acid-base balance and alteration of their physiological functions have been observed, while organisms with calcium carbonate structures (e.g. shells, skeletons) may experience dissolution of their forms (Cummings et al., 2019). Conditions of lower pH and/or higher temperature can affect directly or indirectly growth, development, reproduction, metabolism, and behavior of marine species, thus impacting their population balance and overall health.

Implications of CC on the sex ratio of species will affect the proportions of females or males able to reproduce, consequently leading to a decrease in the active population (Padilla-Gamiño et al., 2022). For example, acidification had an impact on the sex ratio of the oyster Crassostrea virginica, as it has been found that the less energetically costly spermatogenesis was favoured in comparison to oogenesis, thus resulting in an increased number of male oysters (Boulais et al., 2017). Asynchronous or delayed gametogenesis might result in decreased fertilization success and larval fitness, which can modify recruitment and limit the expansion of oyster reefs thus eliminating the valuable ecosystem services derived from those habitats (Boulais et al., 2017). Low pH experimental trials had no significant influence on the fertilization success and the initial growth of the mussel Mytilus edulis larvae, however, these larvae were 28 % smaller than the control ones after two months (Bechmann et al., 2011). In contrast, exposure of the mussel Musculista senhousia, under low pH conditions, resulted in eggs of bigger size indicating increased maternal care and more resilient larvae (Zhao et al., 2019). Acidification affects the quality of the abalone Haliotis iris juveniles' shell, causing dissolution and thinning, with possible consequences for resistance against physical pressures like predation and wave impact (Cummings et al., 2019).

Low pH experimental conditions in the Mediterranean coral *Astroides calycularis* caused a delay in spermacy development and a persistence of mature oocytes, thus restricting or interrupting the fertilization process and leading to a lack of embryos (Marchini et al., 2021). The effect of low pH on shrimp larvae *Pandalus borealis* larvae caused a significant delay in zoeal development time (Bechmann et al., 2011). The gonadosomatic index of the female sea urchin *P. lividus* was lower under low pH, indicating a reduced allocation of energy towards reproductive activities (Marceta et al., 2020). Mos et al. (2020) indicated that larvae of the sea urchin *Centrostephanus rodgersii* during metamorphosis had a higher percentage of anomalies and less number and smaller length of spines and pedicellaria at low pH conditions.

The disruption of normal behavior processes in marine organisms is often the result of an altered metabolic path, and may affect the ability to carry out fundamental activities such as escaping predators, feeding, competition, and obtaining mating opportunities (Briffa et al., 2012). Wright et al. (2018) indicate that acidified conditions may alter the shell morphology and the metabolic reaction of the oyster C. gigas in the presence of a predator and thus increase its "visibility" as prey. The bivalve Abra alba almost stopped suspension feeding under reduced pH in order to eliminate the intake of low pH water, while the polychaete Lanice conchilega increased its pumping frequency, thus suggesting higher metabolic demands (Vlaminck et al., 2022). Low pH levels deteriorated the escape behavior of the conch gastropod Gibberulus gibberulus gibbosus, as a result of a decision-making impairment, caused by a neurotransmitter receptor dysfunction due to the increased CO₂ (Watson et al., 2014). Herbivore gastropods might be characterized by increased consumption rates but, at the same time, decreased movement and less effective escape behaviors (Bass and Falkenberg, 2023). Hermit crab Pagurus bernhardus, exposed to acidified conditions, reduced their ability to receive information and decision making, thus indicating impaired selection behavior (de la Haye et al., 2011). In another study, hermit crabs under low pH treatment were less effective in locating their food source and showed lower rates of antennular flicking used for

chemoreception (de la Haye et al., 2012).

Impacts and threats on benthic communities (key drivers)

- Degradation and finally destruction of subtidal macroalgal communities (OW + MHWs)
- ullet Habitat and biodiversity loss over extended areas and depth zones (OW + NIS)
- Increase of regime shifts and anoxic episodes in coastal lagoons (OW + desertification)
- Mass mortalities and disappearance of formerly abundant native species (OW + MHWs)
- Establishment of the "MHWs MMEs/mortality rates" synergy (MHWs)
- ullet Increased occurrence of pathogenic agents (OW + water circulation)
- Degradation of Marine Animal Forests (OW + MHWs + MMEs)
- Coral bleaching (OW + MHWs + OA)
- Coral regeneration following injury may be hindered (OW + OA)
- Increased presence of trace elements may reduce the coral's resistance to heat stress (OW)
- The sex ratio of species will be affected, thus reducing the active population size (OA)
- Asynchronous or delayed gametogenesis may decrease fertilization success and larval fitness (OA)
- Poor quality of juveniles' shells can affect their resistance to physical stresses such as predation and wave action (OA)

2.2. Plankton communities

Marine plankton at the base of the ocean's food web reflects the state of the wider pelagic environment. The impact of CC on plankton communities remains inadequately comprehended, although data from the integration of mesocosm experiments, fieldwork, and ecosystem modeling have indicated that the rapid OW and OA during recent decades have affected the distribution patterns of marine plankton communities.

2.2.1. Pico-, nano-, micro-plankton

Oligotrophic EM is characterized by the key role of the microbial food web in biomass production and transport to upper trophic levels. There is experimental evidence that, in a warmer ocean, planktonic communities will decrease their average body size, with microbes playing a dominant role in the carbon cycle (Sarmento et al., 2010). At high temperatures, microbial communities exhibit increased productivity; however, they likely experience a decrease in biomass stocks due to significant export events that diminish nutrient availability on the sea surface, leading to shifts in community structure and a higher proportion of heterotrophs to autotrophs (Archibald et al., 2022). In the Adriatic Sea, a time series of several microbial parameters showed that the microbial food web's response to temperature variations is consistent over time, irrespective of trophic status; temperature increase was correlated with microbial heterotrophic activities such as a rise in bacterial growth and an increase in the abundance of bacterial predators, accompanied with a growing importance of autotrophic picoplankton (Šolić et al., 2018).

Reduction in body dimensions as temperature rises is widely known as Bergmann's rule (Sommer et al., 2017). Phytoplankton average cell sizes turn smaller in warmer waters, although size shifts can be explained by metabolic factors and also by top-down effects. Peter and Sommer (2013), using natural phytoplankton experiments, show that the cell size of most species as well as the community mean cell size diminishes with temperature under all grazing schemes. In a similar study, Sommer et al. (2017) report that when smaller algae dominate a phytoplankton community, a higher amount of primary production (PP) will be respired within the microbial food web and thus a reduced proportion of PP will be directed towards the traditional food chain involving phytoplankton, zooplankton, and fish; this indicates a decrease in ecological performance, which ultimately leads to a decline in the export of PP through sedimentation, reflecting a drop in the effectiveness of the biological carbon pump.

The occurrence of MHWs is anticipated to rise in the EM; in a

Mediterranean lagoon, during a mesocosm experiment, it was evident that MHWs (+5 °C compared to the controls) have significant effects on plankton communities (Soulié et al., 2023). Gross primary production (GPP), respiration (R), phytoplankton growth (μ), and loss (L) rates significantly increased by seven to 38 %, whereas the phytoplankton succession was altered with the dominance of cyanobacteria and chlorophytes.

The impact of MHWs on phytoplankton is particularly significant, as they are a crucial source of carbon, nitrogen, phosphorus, and essential fatty acids within aquatic ecosystems. Kim et al. (2024) demonstrated that zooplankton that consumed "HW" phytoplankton (i.e. phytoplankton grown under heatwave conditions) produced lower biomass than those fed on "ambient" or "constant warming" phytoplankton, due to the lesser C, N, P and fatty acid concentrations contained in the first.

As a general trend, microbial communities in oligotrophic waters, such as phototrophic pico- and nano eukaryotes are considerably favoured by OA, when compared with a non-significant response of larger autotrophic prokaryotes, under nutrient-rich conditions (Sala et al., 2016). Throughout a 10-day mesocosm experiment in the EM where the pH was reduced by \sim 0.3 units and temperature elevated by \sim 3 °C the *Synechococcus* density amplified in response to warming, while the SAR11 bacteria clade was favoured by the combined acidification and warming (Tsiola et al., 2023). Similarly, in the Thai Lagoon, in warmed mesocosms of +3 °C the dominance of picophytoplankton was striking, including *Prochlorococcus*-like and *Picochlorum*-like cells whereas, increased numbers of nanophytoplankton, cyanobacteria, bacteria, viruses as well as previous blooms of cyanobacteria and picoeukaryotes have been recorded (Courboulès et al., 2021).

Coccolithophores represent a category of calcifying phytoplankton that can attain high densities in the MS and their responses to OA are affected by temperature and nutrient availability. D'Amario et al. (2020) suggest that the OW and MHWs will cause a rapid reduction in EM coccolithophore populations, with these effects being intensified by OA. Performing a land-based mesocosm experiment, they found that coccolithophore density extremely decreased under the combined OA/temperature increase and Emiliania huxleyi calcite mass decreased consistently; moreover, coccolith malformations were common under OA. Living coccolithophore communities have been explored off Methana, Eastern Peloponnese (Greece), along a pH gradient created by natural CO2 leaks; high numbers of holococcicolithophore species dominated the surface waters and in particular, Algirosphaera robusta, unaffected by the low pH environment, while changes in the community structure were associated with increased temperature and nutrient content (Triantaphyllou et al., 2018).

EM is projected to be influenced primarily by alterations in water circulation, with an anticipated rise in surface water productivity (Macias et al., 2015). Projections in modeling for the Aegean Sea suggest a rise in primary productivity, which is expected to shift from its current oligotrophic state to a mesotrophic one (Sgardeli et al., 2022).

Conversely, in the Middle East region, where temperature in 2090–2099 (compared to the baseline of 1990–1999) is expected to surpass the global threshold of 3.64 °C, a side effect of OA will be a decline in primary productivity (Cooley et al., 2009; Bopp et al., 2013), as well as, OA is anticipated to cause significant alterations in phytoplankton populations (Dutkiewicz et al., 2015). Roxy et al. (2016) confirm these findings and report a decrease of 20–30 % in surface chlorophyll levels over 60 years.

2.2.2. Meso-, macro-plankton

Time series data are essential to explore the state of plankton communities and to predict fluctuations that may impact the overall food web. Semmouri et al. (2023), analyzing time series data from 2009 to 2022, discovered a notable decline in abundance, reaching as much as two orders of magnitude, in four predominant copepods (*Temora longicornis, Acartia clausi, Centropages* spp., Calanus helgolandicus). The identified MHWs during the summer months, aligned with instances of

population declines, were proposed as the reason for the noted reductions in copepod abundance; the physiological thermal boundaries of the individuals were the likely drivers of these declines. This was the first study reporting such dramatic impacts of MHWs on zooplankton in shallow coastal areas.

Ensemble niche modeling has emerged as a widely used approach for predicting shifts in community composition; in marine research, predictions have typically concerted on taxa at the upper level of the food web, often neglecting plankton. Benedetti et al. (2018), assessing the habitat fitness of 106 copepod species, indicate that nestedness alongside a decrease in species richness is the primary pattern influencing the distinction between current and future copepod communities in the MS; they highlighted the uncertainty in modeling methodology, but they also emphasized its value for understanding zooplankton community shifts.

Using multiple environmental niche modeling, a comparatively small decline in species richness (about 7.42) has been forecasted for 97 % of the MS surface populations, with greater losses anticipated in the eastern areas (Benedetti et al., 2019). It was also suggested that CC is unlikely to change the distribution of copepod functional traits in the MS, as most of the species (both more sensitive and less sensitive ones) are functionally redundant, and this is expected to mitigate the loss of ecosystem functions (Benedetti et al., 2019). The species most adversely affected are linked to temperate environments and have Atlantic biogeographic roots; therefore, these findings align with the concept of progressively more tropical Mediterranean communities.

Benedetti et al. (2021) employed species distribution models for 336 phytoplankton and 524 zooplankton species to assess their current and upcoming habitat fitness trends. By the century's end, in a high-emission scenario, they expect a general rise in plankton diversity due to OW along with a poleward movement of species' dispersal. Phytoplankton diversity is expected to rise by over 16 % in most areas, except for the Arctic Ocean. On the contrary, the zooplankton diversity is expected to experience a slight decline in the tropics, while it is forecasted to rise significantly in temperate to subpolar regions. At these latitudes, it is anticipated that almost 40 % of the phytoplankton and zooplankton communities will be substituted by species migrating toward the poles. Changes of this nature could interfere with plankton-driven processes, such as carbon capture and storage.

Zooplankton reactions to the OW also encompass changes in phenology, geographical dispersal, and body dimensions, along with the consequences of their interactions with other trophic levels. Phenology largely depends on thermal preferences, optimal temperature ranges, and adaptability. In a warming climate, organisms have generally migrated towards the poles and/or into deeper waters to stay within their preferred temperature ranges; however, these alterations are not steadily observed, exhibiting considerable variation in intensity and direction, and are frequently specific to individual species (Ratnarajah et al., 2023). In addition, reductions in body dimensions have been identified as the third widespread reaction to CC. Research on marine copepods, the most prevalent multicellular marine organisms on the planet, documented that temperature emerged as a more crucial determinant of body size, than latitude or oxygen levels, demonstrating a 43.9 % decline within a temperature spectrum of 1.7-30 °C (Ratnarajah et al., 2023). Benedetti et al. (2025) anticipate that CC will stimulate trait homogenization of marine planktonic copepods, potentially leading to a reduction in mesozooplankton biomass and ultimately to a decline in the efficiency of carbon export.

Regional studies add depth to these findings. Berline et al. (2012) using six mesozooplankton time series collected across MS, detected an increase in zooplankton abundance alongside a decline in chlorophyll in the Aegean Sea (Saronikos Gulf); this shift was linked to the decrease in human-induced nutrient contributions, a rise in microbial elements, and an intensified grazing pressure on phytoplankton, driven by environmental variability.

Villarino et al. (2020) explored the relations between rising sea

temperatures and shifts in copepod community structure over the past 30 years (1980–2012), utilizing zooplankton time-series data from three locations: two in the eastern North Atlantic (Bay of Biscay, Kattegat Sea) and one in the EM (Saronikos Gulf). Their findings indicate that in the Kattegat and Saronikos Gulf, where the temperature rise was most significant among the studied areas, the changes in the copepod community were closely associated with temperature changes, demonstrating that species tend to adhere to their thermal ecological niche over time.

Kalloniati et al. (2023), examining the long-standing shifts in plankton biomass and growth timing (phenology) in the Saronikos Gulf over 26 years from 1988 to 2015, document a clear interaction between temperature increases and alterations in ecological status. During the period of elevated nutrient input (1989-2004), a temporal discordance between zooplankton and phytoplankton was noted, along with a positive correlation between zooplankton growth and temperature; in the subsequent warmer, less nutrient-rich interval (2005–2015), zooplankton growth occurred earlier in tandem with phytoplankton growth. Ultimately a sudden negative interannual relationship between temperature and mesozooplankton was identified, alongside a decrease in summer biomass associated with cladoceran numbers. These findings imply that ongoing OW could impact both, plankton abundance and phenology in the coastal eastern Mediterranean, potentially leading to changes in plankton community structure and resulting in a subsequent "domino impact" on the upper trophic levels.

In the Levantine Sea (EM), Ouba et al. (2016) note a significant rise in zooplankton numbers tied to thermohaline circulation changes, highlighting the significance of hydrological changes driven by climate factors. They underscored the complex relationship between climate-induced hydrological changes and zooplankton behavior, stressing the importance of continuous monitoring for accurately identifying long-term patterns.

Batistić et al. (2014) examine the possible links over the last 20 years between mesoscale circulation patterns in the Ionian Sea and the emergence of recently recorded species, in conjunction with the sea temperature rise within the Adriatic Sea. They discovered that the shifts in the zooplankton community were associated with the circulation patterns in the Northern Ionian Gyre likely due to the influx of Modified Atlantic Water into the Adriatic, whereas, the occurrence of Lessepsian species was linked to the cyclonic formation, which regulates the flow of EM waters. As a result, new species now significantly contribute to the zooplankton assemblages in the southern Adriatic, and in some instances, have supplanted local species. These findings highlight the influence of oceanic circulation on species introductions and emphasize the potential for upcoming colonization occurrences driven by climate-related changes in circulation patterns.

Garcia et al. (2025), examining a zooplankton time series from 2006 to 2022 in the Marseille Gulf, report that CC promoted a rise in the populations of two warm-water copepods (Corycaeidae and *Temora stylifera*), while negatively impacting a cold-water one (*Calanus helgolandicus*).

In the Western Mediterranean, OW and reduced predation pressure are believed to be the primary factors influencing mesozooplankton variability (Yebra et al., 2022); furthermore the predominant species of zooplankton are suggested as biological indicators for future research concerning climate variations and alterations in zooplankton communities (Fernandez de Puelles et al., 2023).

Human-generated CO_2 releases contribute to OA, OW, and increased stratification; the overall impact of these processes on marine plankton calcifiers over eras of decades to centuries is not well comprehended. Pallacks et al. (2023) examined how pelagic foraminifera, inhabiting the sea surface, react to rising atmospheric CO_2 levels; their findings indicate that higher levels of human-induced CO_2 resulted in significant reductions in size and weight due to alterations in shell formation. They expect that further rises in atmospheric CO_2 will lead to continued declines in calcification processes by marine organisms within MS.

The significance of taking into account the thermal history of species

has recently been emphasized in the context of forecasting how copepod populations will respond to CC-related events, including either steady OW or MHWs; it is demonstrated that species, having experienced different thermal conditions, may show differing levels of resistance to anticipated temperature rises (de Juan et al., 2025).

Indicating that the combined impacts of concurrent stressors impose costs hindering fitness recovery while still supporting elasticity, de Mayo et al. (2023) report that concurrent OW and OA restrict copepod population fitness. Furthermore, Sullaway et al. (2025) document significant CC-related alterations in copepod phenology and reproduction, which ultimately control their population dynamics. Zervoudaki et al. (2024) observed that MHWs increase harpacticoid copepod abundance causing oxidative stress and altering community composition in the Thau Lagoon (MS); these findings indicate that MHWs may shift coastal zooplankton dynamics from calanoid dominance to schemes featuring meroplankton and harpacticoids.

Large populations of Rhopilema nomadica, an extremely venomous scyphozoan, introduced to the MS via the SC, have been prevalent along the Israeli shores during summer and winter seasons since the middle of the 1980s. Although there is a lack of information from the originating population in the RS, the considerable diversity within the population and the various cytochrome oxidase I haplotypes provide evidence, aimed at the concept of numerous introductions or a passage that consistently receives a flow of propagules (Giallongo et al., 2021). Dror and Angel (2024) investigated how temperature influences the various benthic life stages, such as polyps, podocysts, and strobilae, in this jellyfish. Elevated temperatures were found to enhance asexual reproduction and the survival of polyps, while sometimes polyps managed to endure temperatures down to 12 °C. They suggest that podocysts primarily enhance the polyp population, thus facilitating swarm formation, and anticipate that the projected CC scenarios will intensify the capabilities and extend the dispersal range of this jellyfish.

Impacts and threats on plankton communities (key drivers)

- Bacterioplankton will take on a primary role in the carbon cycle (OW)
- The biological carbon pump efficiency will be decreased (OW)
- The nutritional quality of phytoplankton as a food source will be diminished (OW + LTWG).
- $\bullet\,$ The coccolithophore populations will be severely reduced (OA + OW + MHWs)
- The EM's current oligotrophic state will shift to a mesotrophic one whereas in the RS primary productivity will drop (OW + OA)
- $\bullet\,$ Dramatic population declines for several copepod species in coastal areas (OW + MHWs)
- Nestedness alongside a decrease in species richness is the primary pattern differentiating current and future copepod communities (OW)
- Body sizes will be reduced with shifts in both phenology and geographical dispersal (OW)
- Upcoming colonization occurrence will be largely driven by climate-related changes in circulation patterns (OW + water circulation)
- \bullet Further increases in CO_2 will lead to continuous declines in marine plankton calcifiers (OA + OW)
- Homogenization of traits among marine planktonic copepods (OW)
- • Species, having experienced different thermal conditions, may show differing levels of resistance to OW (OW + MHWs)
- Concurrent OW and OA will restrict the fitness of copepod populations (OW + OA)
- Projected CC scenarios will intensify the capabilities and extend the dispersal range
 of the invasive venomous jellyfish R. nomadica (OW)

2.3. Non-indigenous species and altered pathways of species introductions

Non-indigenous species (NIS) are considered any organism introduced outside its natural range. The part of NIS that may impact or threaten biodiversity and ecosystem services, are considered and called invasive alien species (IAS) (EU, 2014).

NIS and IAS, being among the major direct drivers of biodiversity change and finally loss (IPBES, 2023; Galil et al., 2021), have raised issues in almost all coastal regions globally, but their impact is most severe in the EM (Galil et al., 2021). According to a recent report on the validated NIS inventories in the MS (Galanidi et al., 2023), Israel and

Turkey are the countries with the majority of reported NIS (457 and 437 NIS, respectively), with Italy (282 NIS), Lebanon (277 NIS), Egypt (266 NIS) and Greece (249 NIS), being next. It is clear that EM is serving as a central point, launching site, and distribution center for their expansion throughout the basin (Galil, 2023), whereas, there is a declining trend westward into the Adriatic and western Mediterranean countries (Galanidi et al., 2023). The SC serves as the primary route for the NIS arrival into the MS; the canal's ongoing expansions have heightened concerns regarding the escalating propagule pressure, leading to the persistent introduction of new Erythraean species, along with the related decline and disappearance of indigenous species, habitats, and ecosystem functions (Galil et al., 2017). There is a prevailing consensus now that "If we do not understand and mitigate the ecological risks associated with the expansion of the Suez Canal, the integrity of a large part of the Mediterranean ecosystem will be in jeopardy" (Samaha et al., 2016). Erythraean algae, invertebrates, and fish have deeply intruded into the structure of the southeastern MS biological communities; their impacts are partly defined by their demographic success (populations and distributional range) (Galil et al., 2021) whereas, at a Mediterranean scale, Mollusca, Arthropoda, Fishes, Macrophytes are represented at highest numbers (Galanidi et al., 2023). Except for a few cases, the influence of IAS on the indigenous Mediterranean populations remains unexamined in scientific studies (Galil, 2023). In the meantime, numerous Erythraean species have emerged as the most prominent inhabitants of Marine Protected Areas throughout the Levantine; their presence has led to the displacement and replacement of native species, ultimately undermining marine conservation initiatives and hindering the recovery of crucial species that are both economically and ecologically significant (D'Amen and Azzurro, 2020).

In the Mediterranean, research associated with invasive species has been constantly increasing during the last decades, with the establishment of several databases (e.g. EASIN, AquaNIS, NOBANIS, MEDMIS, DAISIE). On the other hand, marine invasion has not received such great attention in the Middle East marine areas, presumably because the phenomenon is not of the same magnitude. Indeed, Lessepsian migration (i.e. the influx of RS-Indian Ocean origin species into the MS) has been, and is still being thoroughly studied, whereas the opposite phenomenon (anti-Lessepsian migration) does not appear in the scientific literature to the same extent with only a few recent works being conducted. According to Galanidi et al. (2023) half of NIS recorded in the MS originate from the Indo-Pacific region and have accessed the basin via the SC. Moreover, 59 % of NIS in the eastern part is Lessepsian migrants, with this percentage becoming lower as we move westwards, indicating the strong effect of the Canal. The introduction of NIS in new biota has been strongly induced by CC, as rising sea temperatures favor the likelihood of introduction, establishment, and expansion of thermophilic species (e.g. Karachle et al., 2022).

The Convention of Biological Diversity (CBD, 2014) has identified and described the potential pathways of NIS introductions across all environments. All pathways have been identified as vectors of introductions in the marine ecosystem. Concerning MS, the prevailing one is corridors, with more than half of the almost 1000 NIS species having entered through the SC, followed by transport–stowaway (Galanidi et al., 2023).

The impacts of marine IAS have been documented and are mainly being identified on biodiversity, ecosystem services (e.g., fisheries, tourism, and industry), and human health. The impacts of IAS are not only harmful but, in some cases, have a positive effect. In a thorough account, Katsanevakis et al. (2014) have mapped the mechanisms with which marine IAS impact biodiversity and ecosystem services. This work was further elaborated by Tsirintanis et al. (2022), including also impacts on human health.

Concerning impacts on biodiversity, these are mainly perceived, as, to date, there are only reports and no actual proof. Indeed, evidence as well as the implementation of ecological indices reveals that IAS, and especially those of Indo-Pacific origin, could either displace (e.g.,

Bariche et al., 2004; Giakoumi, 2014), narrow the trophic niche (e.g., Stergiou, 1988), and/or decline the biomass of local species (e.g., Bariche et al., 2004; Arndt et al., 2018) through competition for space and resources, and result in ecosystem and habitat degradation (e.g., Tsirintanis et al., 2023). Nevertheless, CC, combined with other anthropogenic impacts, may induce extinction and/or extirpation of native species (e.g., Cheung et al., 2010; Robinson et al., 2019).

Food provisioning, recreation, and tourism, as well as symbolic-aesthetic values are the most negatively impacted ecosystem services. Aquaculture and fisheries are affected by IAS in a wide variety of ways (e.g., Katsanevakis et al., 2014; Huseyinoglu et al., 2023; Tsirintanis et al., 2022; and references therein): (a) algal blooms, (b) macroalgal and 'sessile species' fouling; (c) damage on fishing gear or catch, for example, due to *Lagocephalus sceleratus* and *Callinectes sapidus*; (d) net clogging by *Rhopilema nomadica* swarms; (e) reduced fisheries yields; and (f) ruin of pelagic fisheries, as in the case of the Black Sea, due to the presence of *Mnemiopsis leidyi*. In certain areas of the EM, reduced biomass of native commercial fishes and, in contrast, increased numbers and biomass of low-value IAS are being recorded with strong effects on fisheries (e.g., Bariche et al., 2004; Arndt et al., 2018; Kondylatos et al., 2023). On the other hand, IAS could be proven as a new fisheries resource increasing the income of fishers (e.g., van Rijn et al., 2020).

When assessing the effects of NIS-IAS on human health, it becomes evident that they are solely detrimental (e.g. Galil, 2018; Tsirintanis et al., 2022); those, impacting human health, belong to Osteichthyes, Cnidaria, and Echinodermata (Tsirintanis et al., 2022). To date, ten species have been documented to cause injuries and poisoning: the fishes L. sceleratus, Plotosus lineatus, Pterois miles, Siganus luridus, Siganus rivulatus, Synanceia verrucosa, and Torquigener hypselogeneion; the hydroid Macrorhynchia philippina; the jellyfish R. nomadica, and the sea-urchin Diadema setosum. Among those species, special attention should be given to L. sceleratus, a fish that entered EM through the SC in 2003 (Akyol et al., 2005) and has already spread across the basin (Coro et al., 2018; Ulman et al., 2021); it is highly toxic, containing a strong neurotoxin (Tetrodotoxin), which if ingested in high concentrations can lead to death. Recently, it has been documented, that this species displays aggressive behaviour, attacking bathers; by 2023, over 28 instances of physical assaults, a minimum of 144 cases of non-lethal poisoning, and 27 human deaths attributed to its ingestion have been recognized in the MS alone (Ulman et al., 2024).

Consequently, the phenomenon of species invasions is strongly related to CC and the increasing OW and is expected to lead to further introductions, establishments, and spreads. Management actions must be taken to avoid the arrival of additional NIS, and measures to be implemented to mitigate the impacts of NIS-IAS on biodiversity, ecosystem services, and health. Such actions should include (Huseyinoglu et al., 2023): (a) prevention of new arrivals, through constant monitoring, information of relevant stakeholders and the public, and the enforcement of regulations; (b) early detection of new arrivals, for proper monitoring and surveillance; (c) management, through removal, control and, if possible, eradication; and (d) adaptation, based on long-term monitoring and exploitation of those species that can be used, e.g. a food recourse, in the aquaculture industry (as fish-feeds), for pharmaceutical uses, and cosmetics.

A study by Galil (2023) reveals that the Egyptian authorities have the ability to decrease upcoming new species invasions. In 2021, Egypt released bids for 17 additional desalination plants with a daily capacity of 2.8 million m³, aiming to reach 6.4 million m³ by 2050; the high-salinity brine waste could create a strong barrier if dumped into the canal (Galil, 2023). Building locks would reduce the movement of propagules carried by the currents through the SC. We propose that this initiative, appearing to be an excellent first step towards mitigation, should be encouraged not only by other nations (not only from MS) but also by international environmental organizations and agencies, over

various approaches, including financial contributions.

Impacts of Non-indigenous species

- The arrival of NIS into the EM is the key direct driver of biodiversity loss
- CC strongly induces these incursions, as OW enhances the chances for the invasion, establishment, and expansion of thermophilic species
- The SC serves as the primary route; its successive enlargements reinforced the continual invasions of new Erythraean species, causing an incessant decline and degradation of native species, their habitats, and the services provided by the ecosystem
- The impact of those species on human health is harmful; so far, ten species have been recorded to cause injuries and poisoning

3. Impacts and threats on fisheries and fisheries resources

Globally, about 9 % of animal food derives from marine fisheries; 39 million people are directly employed in it, and about four times that number in dependent industries (FAO, 2020). However, the effect of CC on fishery resources is already present and predisposes to the degradation of the above numbers. CC can affect fisheries in a multitude of ways: OW may trigger distributional shifts, forcing marine organisms to seek water masses within their temperature tolerance limits; poleward migration or occupation of deeper water strata have been documented (Cheung et al., 2009; Nye et al., 2009; Perry et al., 2005). OA most commonly affects shellfish fisheries (Gazeau et al., 2007; Narita and Rehdanz, 2017), however, its impact on phytoplankton (Berge et al., 2010) can disrupt the whole marine food web, leading to declining primary productivity (Chust et al., 2014) and in turn lower fisheries yields (Cooley and Doney, 2009). Storminess is a climate stressor disturbing marine life and habitats, with a potential negative consequence on fisheries yield and the welfare of coastal populations. Storms affect fishing activities, compromise security at sea for fishers, and threaten their vessels and gears, as well as the land-based infrastructure. Sea Level Rise will result in the loss of key coastal habitats (e.g. estuaries) serving as nurseries for several commercial species and a decline in fisheries production (Perry et al., 2005).

Alterations in seawater temperature and chemical composition due to CC (IPCC, 2022) can trigger diverse physiological responses in marine fishes such as disruption of the reproductive cycle (timing and success of spawning) and reproductive fitness (Pankhurst and Munday, 2011), development rate of eggs and larvae (Petitgas et al., 2013), sex determination (Geffroy and Wedekind, 2020), aromatase synthesis and activity, thus affecting the reproductive cycle, sexual differentiation, and the sexual inversion process in several fish species (Brulé et al., 2022), and even the evolutionary changes to adapt in a changing environment (Nagelkerken et al., 2021, 2023). Other consequences of CC on marine habitats, such as expansion of the Oxygen Minimum Zones and disruption of ocean circulation, can affect the connectivity among fish populations.

The impacts of OA on the metabolism of teleost fish are related to the habitat type, with benthic and stenohaline species being more sensitive. Cattano et al. (2018) indicate that under acidified conditions, fish larvae are attracted to the smell of their predators or they miss their capability to sense and detect them (Munday et al., 2010; Dixson et al., 2010). Fish predators are also adversely affected and might present avoidance behavior in the presence of injured prey (Cripps et al., 2011). Fish reared under acidified conditions were characterized by a higher activity rate, and they spent less time in their shelter, therefore becoming more susceptible to predation risks (Munday et al., 2010). According to Domenici et al. (2012), individual lateralization (the decision of fish to turn either left or right) is disrupted under acidified conditions, thus providing evidence that brain function in larval fishes is affected, together with a series of relevant cognitive tasks.

Mediterranean fisheries (MF) have specific unique characteristics: (i) high diversity of catches, (ii) a high number of captured species (200+commercially exploited species (FAO, 2024)), (iii) lack of major single

stocks, (iv) reduced body size of specimens (Mediterranean nanism ("dwarfism", Tortonese, 1951) and (v) small scale vessels (>80 % of <12 m in length). Caddy (2009) aptly defines MF as "fisheries for juveniles". MF have experienced a rapid expansion during the 20th century, progressively resulting in declining catches (FAO, 2022). To date nine out of 13 currently assessed stocks in the EM region have fishing mortalities more than twice the target for achieving sustainable exploitation (FAO, 2022).

However, only recently the plausible contribution of CC in this alarming stock status has been investigated. MS is storing an excessively large inventory of anthropogenic carbon while warming faster than other ocean regions (Khatiwala et al., 2013; Adloff et al., 2015). It is suggested that MF vulnerability to CC is exacerbated by factors such as overfishing, increased exposure to OW, the introduction of NIS, and a generally reduced capacity to adapt (Hidalgo et al., 2018). A recent Climate Risk Assessment (CRA) suggests that countries in the southeastern MS are particularly susceptible to the impacts of CC, with Egypt and Tunisia exhibiting the highest levels of risk (Pita et al., 2021).

OW is causing an expansion of the tropical jellyfish range, triggering 'regime shifts' such as from fish to jellyfish. The increasingly high number of gelatinous plankton blooms has given room for questioning whether "a Mediterranean Sea full of jellyfish is a probable future"; jellyfish jeopardize, among others, the economic viability of fisheries as they consume larvae of commercial fish species (Gravili, 2020).

Gkanasos et al. (2021) report that sardines and anchovies in the north Aegean Sea, react negatively to a temperature increase, with anchovies being more affected. Comparably, environmental suitability for valuable commercial cephalopods is decreasing in the MS with their favorable areas rapidly shifting to North European waters (Schickele et al., 2021), while even local extinctions of small pelagic fish populations in the south-east MS are considered probable (Schickele et al., 2020). In contrast, the round sardinella population in the north Aegean Sea showed a 30-fold increase since the early 1990s, positively associated with sea surface temperature (SST) (Tsikliras, 2008).

Similar models predict "winners" and "losers" species on a long-term scale (Moullec et al., 2019; Tsagarakis et al., 2022; Papantoniou et al., 2023; Keramidas et al., 2024). The overall biomass of the upper trophic level species, including fish and macroinvertebrates, is anticipated to grow by 5 % and 22 %; concurrently, the total catch is expected to increase by 0.3 % and 7 % during the periods of 2021–2050 and 2071–2100, respectively (Moullec et al., 2019). The majority of the rise in both catch and biomass is expected to occur in the southeastern region of the MS. Winner species would predominantly belong to the pelagic category, exhibiting thermophilic and/or exotic characteristics, typically smaller in size and placed at the lower trophic levels; loser species would be typically larger and certain ones holding significant commercial value.

Re-organization of communities and changes in the composition of fishery catches (Tzanatos et al., 2014) have been attributed to regime shifts, triggered by a warming climate (Damalas et al., 2021). Although an increase in PP in the EM is presently regarded as the most probable course (Lazzari et al., 2014; Macias et al., 2015), recent studies propose that the PP tendency in the EM may be declining (Richon et al., 2019). Other projections in the Aegean Sea foresee an increase in PP; mullet stocks might be favoured, while the European hake stock is expected to decline (Sgardeli et al., 2022). In the Mediterranean Egyptian waters, the mean temperature of catch (MTC) has increased by a yearly mean of 0.07 °C each year since 1987 (Khalfallah et al., 2023), showing that thermophilic species are favoured. A similar increase was found in the Mediterranean Turkish waters, reaching 0.48 °C per decade (Keskin and Pauly, 2018). However, a Mediterranean-wide study (Peristeraki et al., 2019), indicates that while elevated MTC values were recorded in the central and eastern areas, there has been no confirmed immediate response from demersal marine communities.

Alien invasions have transformed the Levantine reefs, and even well-managed marine reserves had little effect on NIS presence (Rilov et al.,

2018). In the previous decades, an increasing proportion of alien fish in biomass and catches off the Israeli coast has been largely attributed to CC (Corrales et al., 2017). There is increasing indication for an enhanced contribution of NIS in the Aegean Sea catches (Zenetos et al., 2011), with a mild replacement of mullets *Mullus* spp. by goatfish *Upeneus* spp. (Bianchi et al., 2014), and of salema *Sarpa salpa* by spinefoot *Siganus* spp. (Giakoumi, 2014), already occurring. These alterations are likely to lead in a reduction of the catch and income of fishers, changes in their activity and a redistribution of fishing effort towards new fishing grounds. As most NIS are mainly found in shallow waters, the most affected will be the small coastal fisheries which make up 83 % of the number of vessels and 57 % of the workforce.

The human-induced CO_2 levels in the MS are elevated compared to the Atlantic and Pacific Oceans at equivalent latitudes, and they also exceed those of other northern hemisphere marginal seas (Lacoue-Labarthe et al., 2016). Early life stages of fish and shellfish may be severely impacted through growth impairment and reduced calcification respectively, posing a significant threat to MF (Rodrigues et al., 2013).

Several fish species tend to reach maturity at a smaller size in warmer waters. Shapiro Goldberg et al. (2019), studying a set of 16 fish species, report that this trend is more pronounced in the southeastern MS, while Legaki et al. (2023) suggested that a large-scale climate-driven environmental regime modification in the eastern Ionian Sea led to a drop in the size at maturity of *Merluccius merluccius*. Given that the size at maturity shapes population dynamics, as well as the stocks' resilience and vulnerability to fishing, its impact on fisheries yields is yet to be investigated.

The cumulative impact of all the above factors may reduce the EM fisheries' Maximum Catch Potential (MCP) by 2050 between ~25 % (low emissions scenario RCP2.6) and ~75 % (high emissions scenario RCP8.5) (Lamine et al., 2023). Farahmand et al. (2023) assessed the sensitivity of commercial species to CC in the MS and showed declines in environmental suitability for most species; temperate-cold species (e.g. common sole) appear the most sensitive species, contrary to temperate-warm ones (e.g., bogue). In the EM, small pelagic fishes and cephalopods were more exposed to CC. Integrating results to the country level, fisheries were found more exposed to CC for Egypt, and most eastern countries (except for Turkey), which also had low adaptation capacity (Farahmand et al., 2023). Moreover, EM fisheries specifics make them extremely vulnerable to CC, as it has been put forward that they have a lower adaptive capacity to change than their northwestern counterparts (Hidalgo et al., 2022).

RS (subarea 51.1) comprises part of the Western Indian Ocean (FAO major fishing area 51). Its oceanographic and biological features are unique, as it hosts extended regions of coral reefs. It holds the earliest documentation of human consumption of seafood (~125,000 years ago; Walter et al., 2000) and is currently a major fishing area for the seven countries alongside its coastline. RS fisheries are multi-gear and multi-species in nature, with artisanal fisheries being the main players contributing half of the catch. More important in social than economic terms, the sizeable small-scale fisheries (~50 % of the fleet) provide employment opportunities and sustain local community "well-being" (Tesfamichael and Pauly, 2016).

In the western Indian Ocean increasing OW has been monitored for over a hundred years, exhibiting a rate of change that surpasses that of any other area in the tropical oceans; SST increase of 0.6 °C between 1950 and 2009 (Hoegh-Guldberg et al., 2014; Roxy et al., 2014). A long-standing OA trend has been apparent during the last decades (Dore et al., 2009). A decrease of sea surface pH by 0.1 is expected, while oxygen concentration (between 200 m and 600 m depth) is projected to increase by the conclusion of the century under the optimistic RCP2.6 scenario (Bopp et al., 2013). A side-effect of acidification will be the PP reduction (Cooley et al., 2009).

In particular, the RS is undergoing an intense and rapid increase in temperature, this being the greatest shift over the past 160 years (Raitsos

et al., 2011). CC caused coral bleaching, decreased coral reef growth, and decline of large corals in the last two decades (Baker et al., 2004; Cantin et al., 2010; Kotb et al., 2008; Riegl et al., 2012; Furby et al., 2013; Tesfamichael and Pauly, 2016). Coral reef ecosystems (encompassing mangroves and seagrass beds), playing a crucial role in providing habitat for fish and supporting coastal fisheries in the area, are currently experiencing unprecedented pressure from OW and OA. Additionally, coastal development and rising sea levels are expected to further exacerbate the pressure on fisheries resources in this area (Fine et al., 2019; Moustafa et al., 2023). Catches of coral reef fisheries will be the most severely affected, threatening the coastal communities as they depend significantly on these fisheries for their livelihoods. Conversely, locally managed artisanal or semi-industrial fishing fleets may encounter serious repercussions unless they adapt and innovate their fishing gear to accommodate the shifting habitat conditions (e.g. fishing deeper; Barange et al., 2018). Studies on the RS fisheries of Saudi Arabia identified a continuous decrease in the total annual catches of iconic commercial species such as groupers and emperors. This alarming fisheries scenario is assumed to be a combined effect of CC, natural fluctuation, and overexploitation (Al-Rashada et al., 2021).

Impacts and threats on Fisheries (key drivers)

- The fish reproduction will be affected either by complete inhibition or by alterations in the reproductive cycle, including changes in spawning phases, sex determination, and growth rates of eggs and larvae (OW + OA)
- The disruption of normal behavior processes in marine fishes, due to the altered metabolic path, may impact the performance of essential tasks such as avoiding predators, feeding, competition, and obtaining mating opportunities (OA)
- The Maximum Catch Potential (MCP) of EM fisheries may be diminished until 2050, between 25 and 75 % (OW + NIS + OA)
- Overexploitation of marine resources, increased exposure to OW, NIS arrival, and a
 decreased overall adaptability upsurge the MF vulnerability (OW + NIS + OA)
- Several fish species tend to reach maturity at a smaller size (OW)
- Catches of coral reef fisheries may be the most severely affected, threatening the livelihoods of coastal communities (OW + OA)
- The total annual catches of iconic commercial species such as groupers and emperors are continuously decreasing (OW + NIS + OA)

4. Impacts and threats on seabirds

Seabird populations are increasingly threatened by invasive predators inhabiting their breeding areas, as well as by incidental deaths caused by fishing practices, and CC-iduced severe weather conditions. CC-induced severe meteorological conditions constitute a significant threat to seabirds concerning the variety of species impacted (a total of 27 % of all species) and average impact (Dias et al., 2019). The persistence of this particular threat has been evident over the last two decades, as demonstrated by a comparison of findings from relevant research (Croxall et al., 2012; Dias et al., 2019).

Seabirds face various threats that may have cumulative effects. The consequences of CC for seabirds are often intertwined with other risks, particularly the loss of food sources attributed to overfishing (Grémillet and Boulinier, 2009; Sydeman et al., 2012). CC is anticipated to influence the spreading patterns of vector-borne pathogens and ectoparasites (Uhart et al., 2018). Thus, it is challenging to fully comprehend the complex interactions among seabirds, oceanographic conditions, prey availability, fishing practices, and disease occurrences.

Various studies reveal that the effects of CC on seabirds are manifested in both direct and indirect ways. Most studies emphasize indirect effects, striving to identify compelling indications linking extended shifts in climatic and oceanographic patterns to seabird populations; they concentrate on how modifications in the organization and dynamics of marine, insular, and terrestrial environments can ultimately affect food accessibility, predation, survival rates, and reproduction success. Moreover, additional research has underscored the direct repercussions stemming from the loss of breeding habitats, alterations in foraging areas, disruptions to migratory pathways, increased costs of thermoregulation, and extensive breeding failures or mass mortality

incidents (wrecks) in wintering locations due to CC-induced severe weather phenomena (Jentsch et al., 2007; Ramirez et al., 2016; McClelland et al., 2018; Rodríguez et al., 2019).

The MS exhibits significant dynamism, driven by several oceanographic elements such as primary productivity, SST, seafloor depth, and human interventions primarily associated with fishing activities. These variables have the potential to limit the availability of prey for highlevel consumers, and consequently, may shape their foraging distribution pattern (FAO, 2016; Piroddi et al., 2017). Ocean productivity plays a crucial role in influencing the foraging behavior of seabirds, potentially resulting in a more efficient approach to food acquisition during their breeding season (Weimerskirch, 2007; Cecere et al., 2014). The MS is also characterized by a notable eastward reduction in chlorophyll-a/PP and rise of SST (Coll et al., 2010), disturbing the productivity at the low food web fragment (phyto- and zooplankton), and therefore the seabirds' foraging success (Peck et al., 2004; Erwin and Congdon, 2007; Ramos et al., 2013; Weeks et al., 2013). Yet, the Greek Seas are recognized for their extensive network of sites that serve as breeding, foraging, and roosting habitats for marine avifauna (Fric et al., 2012; Thanou, 2013; Zakkak et al., 2013; Karris et al., 2017, 2018a; Xirouchakis et al., 2017).

The expectation is that a scarcity of prey close to seabird colonies in the EM will drive breeders to embark on lengthy foraging journeys to find the most productive feeding grounds necessary for nourishing their chicks and addressing their energy demands (Cecere et al., 2014). Moreover, the harmful CC consequences on fish populations might reduce the accessibility of fishery discards for scavenging seabirds. For instance, Scopoli's Shearwater (Calonectris diormedea), Yelkouan Shearwater (Puffinus yelkouan), Mediterranean Shag (Gulosus aristotelis desmarestii) and Yellow-legged Gull (Larus michahellis) are prevalent in the Ionian Sea, where they are recognized to feed on remnants left by fishing activities consistently or occasionally (Bicknell et al., 2013; Karris et al., 2018b), while Audouin's gull (Ichthyaetus audouinii) shows scavenging habits in the Aegean Sea (Fric et al., 2012). Operations of bottom trawler fisheries in the Ionian Sea were recorded to provide an excessive yearly amount of benthopelagic prey for consumption by shearwaters in the spring, during their pre-laying phase (Karris, 2014; Karris et al., 2018b). These food subsidies resulting from human activities are typically seen as inaccessible as a result of the foraging habits of pelagic seabirds such as Scopoli's Shearwater, and may also be exaggerated by OW as it was lately found in a boundary area among Atlantic and Arctic Oceans (Emblemsvåg, 2022). Therefore, local alterations (e. g. the case of the Ionian Sea) on the structure and amount of demersal trawling discards due to CC may influence the population trends of regional colonies, such as that of the Strofades island complex, hosting 50 % of the species population in Greece (Karris et al., 2017).

The reproductive success of colonial seabirds in the EM can also be influenced by large-scale climatic events, such as El Niño/La Niña, the Southern Oscillation (ENSO), and the North Atlantic Oscillation (NAO), by affecting abiotic elements including SST, rainfall, and the frequency of storms (Cane, 1983; Ottersen et al., 2001). In particular, the association of intense ENSO events with the tropical North Atlantic can alter the production of marine systems and the supply of fish stocks, resulting in negative repercussions for seabird populations (Grosbois and Thompson, 2005; Casselman et al., 2023). A pertinent study reveals that the La Niña phenomenon is connected to diminished survival rates of Scopoli's Shearwater in their wintering areas, leading to an adverse effect on breeding success in a population located in the central MS (Boano et al., 2010). However, certain research indicates that OW may have no effect on the vital rates or population sizes of petrels and shearwaters, which is also true in the MS (Rodríguez et al., 2019).

A further dimension of the negative consequences associated with CC-induced severe weather is the potential flooding of breeding colonies on islands and islets, caused by rising sea levels and/or heavy rainfall storms (Dias et al., 2019). This threat may have substantial implications for coastal bird populations, especially the Mediterranean Shag, which is

limited to the MS and Black Sea, residing in more than 400 colonies (Bazin and Imbert, 2012), as well as for pelagic seabirds, including petrels and shearwaters that establish their nests in low-lying coastal zones (Karris et al., 2024), and may place local populations at hazard in the decades to come.

Dias et al. (2019) indicate that the major proportion of seabirds impacted by CC-induced severe weather conditions are also affected by other threats, namely by-catch incidental mortality, overfishing, and hunting/trapping. This indicates the importance of evaluating (e.g. Karris et al., 2013) and addressing effectively these supplementary threats to compensate for the potential impact of CC. Additionally, adequate conservation measurements and assessments at the local level require essential understanding (e.g. reproductive success, breeding timing, migratory behavior, and foraging approach) which may serve as reference line data for evaluating the OW impact on marine birds in the EM. Subsequently, a sustained research initiative should focus on acquiring that essential knowledge for investigating the consequences of CC on seabirds.

Impacts and threats on Seabirds

- CC-induced severe weather is a critical threat to seabirds, influencing a large variety of species (27 %).
- Alterations in the spreading patterns for the related vector-borne pathogens and ectoparasites will be a potential threat.
- The insufficient prey resources surrounding the seabird colonies in the EM will
 drive breeders to embark on prolonged foraging trips.
- Local changes in the variety and the number of discards resulting from demersal trawling operations may severely impact the population dynamics of local colonies
- The submergence of breeding colonies on islands and islets, linked to the increased sea levels and/or extreme storm-related rainfall, will be another threat.

5. Metal toxicity

Both OW and OA could trigger biological responses in marine organisms related to their growth, metabolism/vital rates, immune defense, fertilization success, as well as contaminants uptake and regulation (Gazeau et al., 2014; Sezer et al., 2020, and references therein; Szalaj et al., 2017). The influence of OA on marine organisms, along with their adaptive responses will significantly determine the future state of marine biodiversity and the functioning of ecosystems. In the forthcoming oceanic environment, marine species will have to contend with acidification while also dealing with other human-related stressors, including elevated pollution mainly in the coastal zone and especially by metals (Giuliani et al., 2020; Nardi et al., 2018; Vizzini et al., 2013; Pascal et al., 2010). Metal pollution could be a significant threat due to industrial and urban activities concentrated in the MS coastal area. Although most trace metals are essential nutrients for organisms, increased concentrations in the marine environment could pose a risk to marine life while food web interrelations could biomagnify the risk of metal contamination. Taking into consideration the additional risk of the 'mercury anomaly' in the Mediterranean (Cossa and Coquery, 2005) enriched with large deposits of cinnabar (HgS), marine organisms are susceptible to mercury accumulation as well (Girolametti et al., 2023).

Acidity plays a significant role in metal solubility and speciation in seawater (Millero et al., 2009) and subsequently in metal bioavailability and uptake by marine organisms (Zeng et al., 2015). It is anticipated that modifications in the sea chemistry resulting from OA may impact the toxicity of both waterborne and dietary metals. Additionally, the adaptation of organisms to the new climatic conditions, including OA, is expected to impact their physiology and metabolic requirements (Ivanina and Sokolova, 2015). The OA effects are species-specific due to the different biology of the organisms (Wilson-McNeal et al., 2020 and references therein; Lewis et al., 2016). The reproduction process and success are considered more vulnerable to OA (Byrne et al., 2010) and even more to multi-stressor exposure to OA and metal pollution (Dorey et al., 2018; Caetano et al., 2021).

It has already been shown that OA and OW could affect both metal (Ag, Cd, Zn) permeability attributes of the eggshell with embryonic metabolic activity of the cuttlefish *Sepia officinalis* (Lacoue-Labarthe et al., 2009) as well as, metal accumulation in the eggs and embryos of the squid *Loligo vulgaris* (Lacoue-Labarthe et al., 2011). The acidic environment increases the solubility of metals from sediments affecting the mobility of metals within sediments and their subsequent bio-accumulation by clams (Lopez et al., 2010). Additionally, metal accumulation by mussels could be increased under the combined exposure to elevated pCO₂ (and the consequent seawater pH decrease), and temperature while it has been shown that OA alone does not pose a threat to elevated metal bioaccumulation (Romero-Freire et al., 2020).

Recently, Qu et al. (2022), Thangal et al. (2023), and Zheng et al. (2023) explored the toxicological consequences of Cu exposure in mussels, Cd exposure in crabs, and Cu exposure in octopuses respectively, under different OA scenarios. It should be noted, that EM people traditionally consume all the above species which are abundant in the coastal zone of the region and available in the fish market; in addition, these species have been widely used as indicators in marine pollution research and could therefore be used as model organisms for multi-stressor metal exposure studies. In the above studies, physiological, cellular, and biochemical biomarkers were evaluated under the aforementioned multi-stressor conditions, indicating that OA can affect metal toxicity, thus revealing an additional risk to marine species and ecosystems' integrity. More specifically, Qu et al. (2022) report that exposure only to OA did not significantly affect the vital rates of clearance and respiration. In the same experiments, oxidative stress biomarkers were activated to protect mussels by both the metallic exposure and OA, although the antioxidant defense mechanisms were not efficient enough to completely protect the organisms, and finally, an increase of lipid peroxidation was also recorded after the exposure to free radicals. The final step in the previous experiment was a quite long depuration period (56 days) during which mussels showed signs of recovery and an improved ability to cope with the combined exposure to OA and Cu (Qu et al., 2022). Crabs exposed to Cd under OA conditions showed a decrease in growth, molting, in the major biological molecules concentration and activation of the oxidative defense system of the organisms while elevated oxidative damage was recorded as well; additionally, Cd toxicity in crabs was increased due to the potential synergistic interaction of OA and metal exposure (Thangal et al., 2023). Cu exposure and OA, synergistically reduced growth and food intake in octopuses, while oxidative damage after Cu exposure was higher due to OA (Zheng et al., 2023). The combined effect of metal exposure and OA altered the transcriptomic profiles (transmembrane transport, mitochondrial, and protein and DNA damages), the microbial community structure within octopuses' intestines, and Cu toxicity though octopuses showed to be well acclimatized when exposed to decreased pH only (Zheng et al., 2023). The toxicity of Cu in mussels and sea urchins in the near future OA was investigated by Lewis et al. (2016); they found that DNA damage in both species was greater when the animals were metal-exposed under OA conditions. Sartori et al. (2023) presented a 20-year time series (from early 2000 to early 2020) of the Cu EC50 on a natural sea urchin population. The effects examined on larval development (including deformities of the arms and abnormalities in the gut formation of the plutei), showed a sharp decrease in the EC50 time series from the years 2016-2017 and onwards (Sartori et al., 2023); Cu EC50 values after 2016 were negatively correlated with surface pCO2 and temperature and positively correlated with pH and dissolved oxygen. The authors explained these results taking into account that the warmest period in Europe, began in 2015 (Lopez, 2021).

As the potential pH decrease in the MS is faster than that of the adjacent Atlantic Ocean (Schneider et al., 2007), it is critical to explore the potential impacts of OA on the EM dominant species exposed to chronic metal pollution in the coastal zone. Such studies might be constantly expanding to include cultivated or endangered species. For example, in the EM, cultivated mussel landings are significant at the

European level. The main coastal areas with mussel cultures in Greece are located in the northern part of the country while regions with lower carrying capacity are distributed along the Aegean and Ionian Seas (Theodorou et al., 2011). Furthermore, shellfish farming is considered a "carbon sink" with low greenhouse gas emissions and has the credit of being a "climate-positive" food product (Bertolini et al., 2023 and references therein). Consequently, the growth and risks of this economically important and environmentally friendly activity under the ongoing CC in the sensitive EM environment should be considered accordingly. Seafood, an important component of the so-called Mediterranean diet, is recommended for frequent consumption due to its health benefits (EU, 2023). Indeed, seafood safety and the nutritional value of the edible marine species under CC are of major concern, especially under the synergistic effects of OA and OW (Lemasson et al., 2019).

Impacts and threats on Metal toxicity (key drivers)

- Acidity plays a key role in metal solubility, mobility, and speciation in seawater and subsequently in metal bioavailability and uptake by marine organisms (OA)
- Crabs, octopuses, mussels, and sea urchins exposed to metals under OA conditions showed an aggravation in several physiological responses, such as decreases in food intake, growth, molting, and major biological molecule concentration, as well as DNA damage (OA)
- Temperature has also been found to increase sea urchin vulnerability to metal exposure (OW)
- OA (alone or in combination with OW) will increase the organisms' vulnerability to metal toxicity, thus revealing a potential synergistic interaction of OA and metal exposure (OA + OW)

6. Knowledge gaps

Reviews using meta-analytical methodologies have indicated specific knowledge gaps which are either correlated to specific species or taxonomic groups, or to specific eco-physiological processes that need to be studied further. For example, Padilla-Gamiño et al. (2022) indicate that crustaceans as a group are less studied regarding the effects of acidification on their reproduction, even though these species constitute a large proportion of the economically important fisheries resources. Specific reproduction traits such as mating behaviour and determination of gender balance have not been sufficiently studied.

Many fish species are inclined to attain maturity at a reduced size in warmer areas (Shapiro Goldberg et al., 2019; Legaki et al., 2023). Considering that the size, at which organisms reach maturity, impacts population dynamics and determines the stocks' strength and susceptibility to fishing, its effect on fisheries yields remains to be further explored.

Fundamental knowledge is missing to be used as baseline data for the identification of CC impacts on marine birds.

Experimental studies on multi-generational, multiple stressors, and species interactions need to be performed to enhance understanding of intricate alterations at the ecosystem level and determine the potential impacts of these changes on ecosystem services under future conditions (Cattano et al., 2018). Long-lasting experiments can allow investigation of the acclimatization capability to CC conditions and thus yield data, that is more significant for predicting future consequences over an extended period. In addition, longer-term experiments involving multiple generations might also enlighten the potential adaptation abilities of some species under CC (Cattano et al., 2018).

Investigation of CC effects under laboratory experimental conditions may have some implications in the understanding and assessment of the impacts on the life traits of marine organisms. As it has already been commented, a series of CC destruction forms, other than OW and OA, can also occur in parallel such as hypoxia for example. Therefore, controlled experiments combining multi-stressors are more favorable and reliable for describing the "big picture" of future scenarios. However, controlled experiments test rather environmental tolerances instead of behavioral preferences which are free to occur in the natural environment (Pankhurst and Munday, 2011).

Finally, the scientific investigation about the influence of NIS on the indigenous MS populations has been limited (Galil, 2023).

7. Conclusions (major threats/factors and mitigation)

Impacts and threats posed solely by OW.

- > An elevated concentration of trace elements could diminish the coral's ability to withstand heat stress
- > Bacterioplankton will assume a central role in the carbon cycle, while the efficiency of the biological carbon pump will be weakened
- > Plankton body sizes will be diminished with shifts in both phenology and geographical dispersal
- > Homogenization of traits among marine pelagic copepods
- > The capabilities and the dispersal range of the invasive venomous jellyfish *Rhopilema nomadica* will be broadened
- > NIS incursions will be expanded, as OW enhances the chances for the invasion, establishment, and expansion of thermophilic species
- > Various fish species are expected to attain maturity at a reduced size
- > Elevated temperatures will enhance the susceptibility of sea urchins to metal exposure.

Impacts and threats posed solely by OA.

- > The sex ratio of the oyster *Crassostrea virginica* will be affected, thus reducing the active population size
- > Asynchronous or delayed gametogenesis may decrease fertilization success and larval fitness of oysters
- > Poor quality of the abalone juveniles' shells can affect their resistance to physical stresses such as predation and wave action
- > The alteration of metabolic pathways in marine fishes due to acidification can disrupt their normal behavioural processes, potentially affecting their ability to perform critical tasks such as evading predators, foraging, competing, and securing mating opportunities.
- > The level of acidity significantly influences the solubility, mobility, and speciation of metals in seawater, which in turn affects the bioavailability and absorption of these metals by marine organisms.
- > Benthic animals subjected to metal exposure under acidification conditions exhibited deterioration in various physiological responses, including reductions in food consumption, growth rates, molting processes, and concentrations of key biological molecules, alongside evidence of DNA damage.

Impacts and threats posed by OW and OA combined.

- > Coral bleaching
- > The process of coral regeneration after sustaining injury may be impeded
- > The existing oligotrophic state of the EM is projected to shift towards a mesotrophic condition, whereas in the RS, a decrease in primary productivity is foreseen
- > Further rise in acidification levels will lead to continuous declines in marine plankton calcifiers
- $\,>\,$ The fitness of copepod populations will be restricted
- > The fish reproduction will be influenced by either total inhibition or modifications in the reproductive cycle, such as variations in spawning periods, sex determination, and the growth rates of eggs and larvae
- > The catches from coral reef fisheries could be among the most adversely impacted, jeopardizing the livelihoods of coastal communities
- OA (individually or in conjunction with OW) will enhance the organisms' susceptibility to metal toxicity, thereby uncovering a possible synergistic relationship between OA, OW and metal exposure

Impacts and threats posed by **OW and MHWs** combined.

- > The decline and final obliteration of subtidal macroalgal communities
- > The mass mortalities and the vanishing of previously plentiful native benthic species
- > Degradation of Marine Animal Forests
- > The nutritional value of phytoplankton as a food source will be reduced
- > Dramatic decreases in the populations of various pelagic copepod species within the coastal zone
- > Pelagic copepods, which have undergone diverse thermal conditions, might exhibit varying degrees of resistance to elevated temperatures

Impacts and threats posed by **OW and desertification** combined.

> The rise in regime shifts and the frequency of anoxic episodes within coastal lagoons

Impacts and threats posed by OW and water circulation combined.

- > The heightened prevalence of pathogenic agents
- > The upcoming colonization events in plankton will mainly be affected by climate-driven changes in circulation patterns.

Impacts and threats posed by OW, NIS and OA combined.

- > The Maximum Catch Potential (MCP) of EM fisheries could be reduced by 25–75 % by the year 2050
- > The overall yearly catches of prominent commercial species, including groupers and emperors, are persistently declining

7.1. NIS and mitigation plan

The interplay between OW and NIS poses the major threat for the loss of habitat and biodiversity across extensive areas and various depth zones in the region. The NIS key route through the Suez Canal (SC) and its continual expansions, have elicited apprehension concerning the growing propagule pressure. Now it's taken for granted that if these environmental hazards are not understood and addressed, a significant portion of the MS may face substantial hazards to its integrity.

Therefore, the proposal concerning the discharge of brine waste into the SC, serving as a high salinity barrier to limit the introduction of new species carried by the currents, appears to be a viable and appealing initial measure towards mitigating this phenomenon. We propose that this action should be encouraged not only by other nations but also by international environmental organizations and agencies, through various approaches, including financial contributions. This initiative, when combined with additional actions designed to mitigate the effects of invasions on biodiversity, ecosystem services, and public health (chapter 4: NIS), represents the crucial next phase in the pursuit of mitigation efforts.

CRediT authorship contribution statement

Epaminondas D. Christou: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Conceptualization. Thanos Dailianis: Writing – review & editing, Writing – original draft, Conceptualization. Evangelia Chatzinikolaou: Writing – review & editing, Writing – original draft, Conceptualization. Paraskevi K. Karachle: Writing – review & editing, Writing – original draft, Conceptualization. Dimitrios Damalas: Writing – review & editing, Writing – original draft. Konstantinos Tsagarakis: Writing – review & editing, Writing – original draft. Evangelia Strogyloudi: Writing – review & editing, Writing – original draft. Georgios Karris: Writing –

review & editing, Writing – original draft. **Soultana Zervoudaki:** Writing – review & editing, Writing – original draft. **Antonia Gianna-kourou:** Writing – review & editing, Writing – original draft. **Maria Salomidi:** Writing – original draft. **Sofia Reizopoulou:** Writing – review & editing, Writing – original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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