Review

Effects of climate change on marine coastal ecosystems – A review to guide research and management

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A R T I C L E   I N F O

A B S T R A C T

There is growing concern over climate models that project significant changes in the oceans, with consequences on marine biodiversity and human well-being. However, marine and coastal ecosystems respond differently to climate change-related stressors depending on the ecosystem, species composition and interactions, geomorphologic settings, and spatial distribution, but also on the presence of local stressors interacting cumulatively with climate change-related pressures. Our paper provides a comprehensive review of the current literature about the effects of climate-related pressures on marine and coastal ecosystems and how local stressors affect their resilience. Our work focuses on key marine and coastal ecosystems from three ecoregions: the Caribbean Sea (coral reefs, mangrove forests, seagrass beds), the Mediterranean Sea (the coral *Cladocora caespitosa*, maërl beds and seagrass beds) and the North-East Atlantic, which include kelp forests, maërl beds, salt marshes and seagrass beds. This review highlights the need for a more comprehensive, multi-species, and multi-stressors approach to predict better changes at the ecosystem and seascape levels of marine and coastal ecosystems. Nevertheless, there is enough evidence to argue that addressing locally key manageable stressors common to multiple ecosystems, such as nutrient enrichment, coastal development, hydrologic disturbances, anchoring or

sedimentation, will reduce the identified adverse effects of climate change. This knowledge is critical for practical conservation actions and coastal and marine spatial management at the ecoregion scale and beyond.

1. Introduction

Despite the implementation of the Paris Agreement, climate models project significant changes in the state of the oceans over the next century with consequences on the entire Earth system, including marine biodiversity and human well-being (Bindoff et al., 2019; IPCC, 2022). Globally, coral reefs, kelp and mangrove forests, salt marshes, seagrass beds and other bio-engineers rank among the most vulnerable marine and coastal ecosystems (hereafter MCE) to climate change (Duarte et al., 2013; Roberts et al., 2017; Spalding et al., 2014). Apart from global stressors, local anthropogenic stressors are also known to severely impact MCEs and can affect the safe operating space, or tolerance, of MCEs to the effects of climate change (Carilli et al., 2009; Scheffer et al., 2015). As a consequence, the combined effects of local anthropogenic stressors make it difficult to define the magnitude of these climate change-related impacts (Bindoff et al., 2019). Rising temperatures and extreme weather events have already affected marine environments globally (Wernberg et al., 2013; Halpern et al., 2015; Poloczanska et al., 2016; Pinsky et al., 2019). While climate change (hereafter CC) cannot be locally managed or contained, local stressors can be (Elliott et al., 2015). Besides, local actions to support healthy natural environments can contribute to CC mitigation and adaptation (Roberts et al., 2017). Therefore, without devaluing the urgency to drastically reduce greenhouse gas emissions into the atmosphere, it is crucial to understand which local stressors (hereafter LS) need to be managed to increase the resilience of MCEs to CC, where resilience is defined as the ability of an ecosystem or species to resist and recover from a disturbance (Holling, 1973). Nevertheless, few studies consider the interactive effects of CC and LS or whether the outcomes of such interactions are species- or ecoregion-specific (Gissi et al., 2021; Furlan et al., 2019).

To address this knowledge gap, this paper aims to provide a comprehensive review of the current literature about the effects of climate-related pressures on MCEs and how local anthropogenic stressors affect their resilience. Our review has been done within the frame of the European Commission-funded project MaCoBioS (macobios.eu). Therefore, it focuses on six key MCEs that are predominant in Europe and its Overseas Territories, covering three ecoregions: North-East Atlantic kelp forests, salt marshes and seagrass beds; Mediterranean coral *Cladocora caespitosa*, maërl and seagrass beds; and Caribbean coral reefs, mangrove forests and seagrass beds. While the conservation interest of seagrasses, mangroves and coral reefs is unquestionable, the inclusion of maërl beds and the single species *C. caespitosa* is not less important. Similar to tropical corals, *C. caespitosa* primarily thrives in shallow habitats and shares the main traits of tropical reef-building corals (Kružić and Benković, 2008; Kersting and Linares, 2012). Moreover, it is one of the best studied bioindicators of long-term climate change effects (Kersting et al., 2013; Kersting and Linares, 2019). For those reasons, this species was deemed more appropriate than other species from the Mediterranean coralligenous assemblages. The ecology of North-East Atlantic and Mediterranean maërl beds has received little attention in contrast to other MCEs (Barbera et al., 2003), but their structural functionality is analogous to kelp forests or even coral reefs, through the complex habitats they provide, supporting a very rich biodiversity. Yet, gathering and consolidating existing knowledge, as well as addressing critical gaps, is paramount for their preservation (Tuya et al., 2023).

These subtidal and intertidal MCEs are among the most productive and valuable ecosystems on Earth, providing habitat for a wide range of commercial and non-commercial species, food and raw materials, coastal protection from storms and erosion, and cultural services, such as tourism and recreative activities (Liquete et al., 2013). Moreover,

some of these MCEs are key contributors to CC mitigation due to their high carbon storage (e.g., seagrasses, mangroves, salt marshes) (Duarte et al., 2013). Nevertheless, these MCEs remain highly vulnerable to the effects of CC and LS (Simeoni et al., 2023). Therefore, studies from all three ecoregions in Europe (Mediterranean, North-East Atlantic), and the Caribbean, were included in this review, to cover a wide range of environmental contexts representative of where strong human pressures and vulnerability to CC drivers combine in threatening MCEs.

The specific objectives of the paper are threefold: to identify the state of knowledge regarding (i) the impact of different CC stressors on key MCEs and (ii) the safe operating space limits of these MCEs, and (iii) to identify key LS that can be managed to reduce the identified adverse effects of CC per MCE framed within its local and regional socioecological context. Such knowledge is critical for practical conservation actions and coastal and marine spatial management at the ecoregion scale and beyond.

2. Literature review methods

A literature review on the Scopus database was conducted, considering any research papers published until December 2021. Search strings for each MCE were constructed in the following form: climate change driver (e.g., climate change, global change, warming, heat wave, acidification) AND local stressor (e.g., impact, disturbance, pressure) AND ecosystem limit (e.g., threshold, tipping point, recovery, loss, shift) AND ecosystem type (e.g., seagrass beds, salt marshes, kelp forests, maërl beds, coral reefs, or mangroves) AND region (North-East Atlantic, Caribbean, Mediterranean). Full search strings are included in the Supplementary material (SM-1). For seagrasses, the literature review focused on the species considered representative of the three ecoregions: *Zostera marina* in the North-East Atlantic, *Posidonia oceanica* in the Mediterranean and *Thalassia testudinum* in the Caribbean. Although the review focused on studies from those three ecoregions, we also included other ecoregions considered relevant, such as the Gulf of Mexico (associated with the Caribbean) or the Arctic (related to the North-East Atlantic). Global studies were considered if they included our study ecoregions. However, we will refer only to the three targeted ecoregions to simplify the reading. Only publications in English were included. In total, 2576 articles were returned by these searches.

Articles were screened according to the following eligibility criteria, (i) studies conducted on the focal species or MCE within a defined geographical area (see above) or results from laboratory and mesocosm experiments, (ii) studies focusing on the effects of CC with or without LS on the selected MCEs. Articles were first screened based on title and abstract, resulting in 705 articles. The full texts of these remaining articles were screened, and 295 articles were retained for this work: 108 focused on coral reefs in the Caribbean; 17 on the Mediterranean coral *Cladocora caespitosa*; 34 on kelp forests in the North-East Atlantic; 13 on maërl beds in North-East Atlantic and the Mediterranean; 50 on mangrove forests in the Caribbean; 25 on salt marshes in the North-East Atlantic and the Mediterranean; 48 on seagrasses in the North-East Atlantic (n = 14), Mediterranean (n = 25), and the Caribbean (n = 9).

When an article included more than one response variable for the ecosystem of interest, each response was included as a separate entry in the results table and referred to as studies hereafter. Therefore, the total number of studies analysed exceeds the number of articles retained. Meta-data, i.e., information describing the study, was extracted from the 295 articles resulting in 946 studies analysed (the complete list of articles from which data were extracted is included in Supplementary material SM-2). Data was compiled in an output table built on the key questions underpinning this review paper: the nature of the study (e.g.,

experiments in fieldwork or laboratory, temporal series, models), the response variables assessed (i.e., the ecological variable measured in the study), the CC drivers and LS, and identification of operational limits or ecosystem tipping points.

Response variables are measurable features of an organism, individual, population, habitat or ecosystem responding to environmental change. A total of 581 response variables were identified and iteratively coded into eight response variable categories to facilitate data analysis: (i) density/abundance (includes survival or mortality), (ii) distribution, (iii) growth, (iv) habitat structure, (v) metabolism, (vi) photosynthesis/ respiration, (vii) reproduction, (viii) other (e.g., "sediment accretion rate", "grazing", or variables related to "paleo-ecology").

The CC drivers of ecosystem change were catalogued as (i) warming, including heatwaves, (ii) extreme weather events, with specific emphasis on storms and hurricanes, (iii) atmospheric CO_2 concentration, (iv) ocean acidification, (v) sea level rise, (vi) salinity (hypo- or hypersalinity), (vii) cooling, reflected by the duration and severity of freezing events, (viii) rainfall regimes, and (ix) inundation. To summarise the general effect of CC drivers on MCEs from multiple studies, we considered the overall effect of a CC stressor to be positive, negative, neutral or unclear when >50 % of the responses were positive, negative, neutral or unclear, respectively (e.g., 60 % negatives and 40 % positives = negative overall effect). An 'unclear' overall effect was assigned when it was uncertain whether the response of a variable was negative, positive or neutral to the ecosystem, population, or individual, and not explicitly specified in the reviewed articles. We visually nuanced the effects between fully (100 %) and mostly [51 %–99 %] positive, negative, neutral or unclear with two shades of colour in the figures. The overall effect was considered 'mixed' if there was an equal number of responses between positive, negative, neutral, unclear, or none of the responses reached a 51 % threshold (e.g., 50 % positive and 50 % negative, or 20 % negative, 40 % neutral, 40 % positive). Details about the exact number of studies per type of effect are summarised in Supplementary materials (SM-3, Figs. S1, S3 and S5).

The LS were classified into 12 categories (Table 1). When interactive effects between CC drivers and LS were tested, the outcome was recorded (i.e., significant interaction or no interaction) as well as the nature of the interaction, if any (i.e., additive, synergistic, antagonistic) and the overall effect (negative, positive, neutral, mixed, unclear) of tested interactions on the MCE. The cumulative overall effect from CC drivers combined with LS was determined following the rules previously described. Details about the exact number of studies per type of effect are summarised in Supplementary materials (SM-3, Tables S2, S4 and S6).

The output table included descriptions of any tipping points or response data that can aid in identifying the safe operating space of the MCE, when such data were reported. Tipping points are understood as the point where following a perturbation, a self-propagated change can eventually cause a system to shift to a qualitatively different state. Safe operating space is understood as the range of environmental conditions that lies between tipping points for which the functioning of the ecosystem remains stable (Scheffer et al., 2015).

3. Results

3.1. Caribbean

3.1.1. Coral reefs

Among all 108 articles, studies of CC effects on Caribbean corals are heavily slanted towards warming (85 % of the studies) (Fig. 1).

Marine heat waves are a primary concern of warming studies (75 %) as they have triggered bleaching events responsible for massive coral mortality worldwide (Eakin et al., 2010; Eakin et al., 2022). Repeated exposure to elevated temperatures can cause general net tissue loss (Neal et al., 2017) and switching to thermal-tolerant symbionts can decrease calcification rates (Ortiz et al., 2013). Sexual reproduction is

Table 1
Proportion of studies per local stressor. N is the number of studies considering both climate change and local stressors.

Ecoregions	Ecosystem	Coastal development	Hydrologic disturbance	Disease	Fishing	Grazing	Invasive species	Nutrient enrichment	Pollution	Recreational activities	Sedimentation	Turbidity	Sulfide stress
Caribbean	Coral reefs N = 77	6 %	–	9 %	13 %	17 %	1 %	11 %	4 %	1 %	6 %	–	–
	Mangrove forests N = 39	2 %	3 %	–	–	–	–	8 %	3 %	–	1 %	–	1 %
	Seagrass beds N = 15	–	–	–	–	–	9 %	–	9 %	9 %	–	–	57 %
Mediterranean	Corals N = 2	–	–	–	–	–	6 %	6 %	–	–	–	–	–
	Maërl beds N = 2	–	–	–	8 %	–	8 %	–	–	–	–	–	–
	Seagrass beds N = 24	4 %	–	–	1 %	–	–	12 %	1 %	1 %	–	–	1 %
North-East Atlantic	Kelp forests N = 48	–	–	–	1 %	8 %	0 %	3 %	–	–	3 %	1 %	–
	Maërl beds N = 6	–	–	–	15 %	8 %	8 %	8 %	–	–	8 %	–	–
	Salt marshes N = 20	5 %	–	–	–	–	1 %	5 %	4 %	–	1 %	–	–
	Seagrass beds N = 65	–	–	–	–	–	–	41 %	–	–	–	–	7 %

Marine & Coastal Ecosystems\n\nCaribbean	RESPONSE VARIABLE CATEGORIES	CLIMATE CHANGE								
		Warming / heat waves	Extreme weather events	Atmospheric CO_2 concentration	Ocean acidification	Sea level rise	Salinity (hyper)	Cooling	Rainfall regimes (reduced)	Inundation
CORAL REEFS	Density/Abundance	20%	25%		4%					
	Distribution									
	Growth	10%	8%		32%	20%				
	Habitat structure	21%	42%		18%	80%				
	Metabolism	6%			7%					
	Photosynthesis/Respiration	9%			18%					
	Reproduction	14%	8%		14%					
	Other	19%	17%		7%					
	Total number of studies	**78**	**12**		**28**	**5**				
MANGROVE FORESTS	Density/Abundance	7%	17%			8%	16%	63%	21%	
	Distribution	10%				23%			7%	
	Growth	46%	22%	100%		54%	50%	5%	36%	67%
	Habitat structure	2%	22%					16%	36%	
	Metabolism	5%				15%	8%			
	Photosynthesis/Respiration	29%	28%				26%	16%		33%
	Reproduction		11%							
	Other									
	Total number of studies	**42**	**18**	**15**		**13**	**39**	**19**	**14**	**9**
SEAGRASS BEDS *Thalassia testudinum*	Density/Abundance	20%	33%				20%			
	Distribution	20%	67%			100%				
	Growth	20%					20%			
	Habitat structure									
	Metabolism	20%					20%			
	Photosynthesis/Respiration	20%					40%			
	Reproduction									
	Other									
	Total number of studies	**5**	**3**			**1**	**10**			

Response Legend

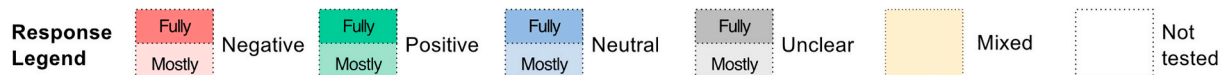| Fully / Mostly Negative	Fully / Mostly Positive	Fully / Mostly Neutral	Fully / Mostly Unclear	Mixed	Not tested

Fig. 1. Summary of studies per climate change drivers and general effects on broad response variable categories in marine and coastal ecosystems of the Caribbean, including the Gulf of Mexico. Percentage values represent the proportion of studies per response variable from the total number of studies per CC driver, indicated in bold for each ecosystem.

critical for resilience, but many studies demonstrated negative effects of thermal stress on coral reproduction, including decreases in larvae survivorship and settlement, inhibition of fertilisation, increased post-settlement mortality and loss of genotypic diversity (LaJeunesse et al., 2009; Randall and Szmant, 2009; Baums et al., 2013; Ross et al., 2013; Davies et al., 2016; Ross et al., 2017); however, inter-species variability is observed (Ross et al., 2013; Randall and Szmant, 2009). In many cases, when temperatures are 1–1.5 °C above the maximum monthly sea surface temperature, increased mortality (Langdon et al., 2018), reduced larvae survivorship (LaJeunesse et al., 2009) and slower healing time (Kaufman et al., 2021) were observed. However, not only the magnitude but also the duration of thermal anomalies is crucial. For example, the number of days at >30.5 °C was the most significant metric characterising bleaching years (Manzello et al., 2007a), although threshold values can be affected by physical or biological factors such as depth or symbiont type (Smith et al., 2016; Buddemeier et al., 2011).

Ocean acidification was the second most studied CC driver (25 % of studies) affecting Caribbean coral reefs. Growth assessments accounted for 43 % of studies and examined the formation or dissolution of coral skeletons, or reef framework, in the face of changes in carbonate parameters, such as aragonite saturation state and dissolved inorganic carbon. Overall, results showed negative effects on coral calcification (Mumby et al., 2013; Camp et al., 2016; Langdon et al., 2018; Martinez et al., 2019), reproduction (Albright et al., 2010; Albright and Langdon, 2011; Davies et al., 2016), and photosynthesis (Bedwell-Ivers et al., 2017; Martinez et al., 2019), but in many cases exhibited neutral (Towle et al., 2015; Bedwell-Ivers et al., 2017; Langdon et al., 2018) or unclear (Kennedy et al., 2013) responses. Akin to thermal stress, some species may be more sensitive to ocean acidification (Langdon et al., 2018; Bedwell-Ivers et al., 2017; Martinez et al., 2019).

Warming and acidification are predicted to interact with each other (Kennedy et al., 2013; Freeman et al., 2013; Buddemeier et al., 2008; Davies et al., 2016). Modelled data suggests that a warming of 2.6 °C reduces cover by 15 %, but when saturation state is considered at CO_2 values for 2100 (710 ppmv), declines in cover reach 41 %–60 % (Buddemeier et al., 2008).

Sea level rise comprised 4 % of studies focused on the ability of coral reefs to protect our coasts. However, with increased sea level, wave energy dissipation is reduced, resulting in enhanced reef erosion (catalogued here as part of growth), compromising reef accretion, and affecting habitat structure (Blanchon et al., 2017; Yates et al., 2017; Wegner and Ellis, 2017; de Bakker et al., 2019).
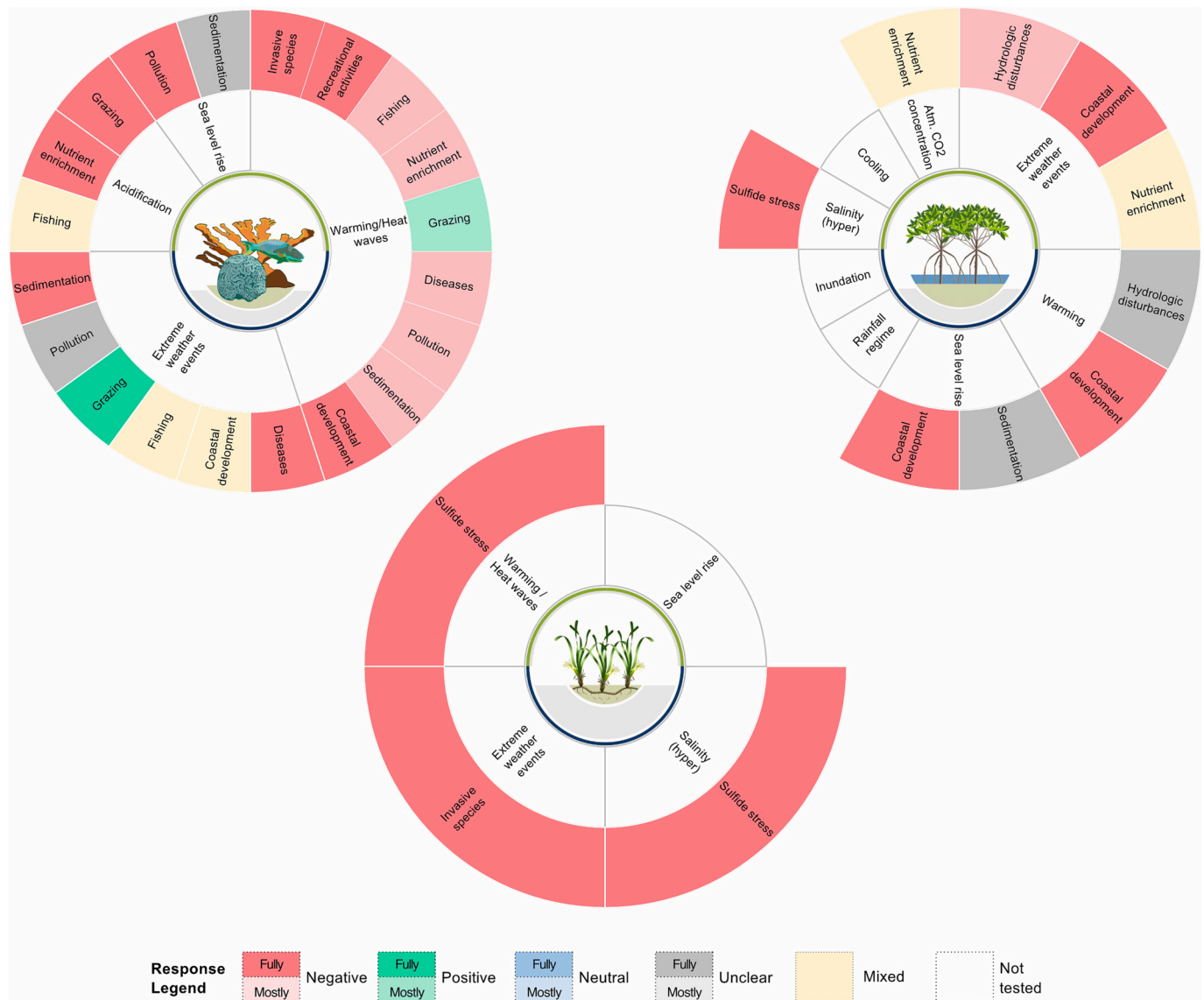

Fig. 2. Cumulative overall effects of local stressors combined with climate change drivers for marine and coastal ecosystems in the Caribbean. Top left: coral reefs; top right: mangrove forests; bottom: seagrass beds (i.e. *Thalassia testudinum*).

Extreme weather events (13 % of studies) are generally negative for corals as they cause physical destruction, resulting in coral cover decline and affecting the number of juveniles and small-size corals (Steneck et al., 2019; Crabbe, 2011). In particular cases, these events can increase asexual reproduction (Foster et al., 2013). The interaction of hurricanes with other climate drivers is complex. In fact, hurricanes can induce local cooling, mitigating the effects of marine heat waves and reducing the recovery time after bleaching (Manzello et al., 2007b).

Studies on the interactive effects of CC and LS have intensely focused on warming, terrestrial run-off (pollution, nutrients, and sediments) and grazing (Table 1, Fig. 2). Higher nutrient concentration, resulting from coastal run-off, acts in synergy with increased temperatures to favour shifts to algal-dominated communities (DeBose et al., 2013) and promote pathological affections (Castañeda-Chávez et al., 2018). The effect of nutrients and thermal stress varied between species and showed mixed effects, such as increased larval settlement and mortality (Serrano et al., 2018).

3.1.2. Mangrove forests

Out of 50 articles, associated studies reported the effects of warming (24 %) and cooling (11 %), hypersalinity (22 %), extreme weather events (10 %), sea level rise (7 %), rainfall regime (8 %), atmospheric CO_2 concentration and inundation (5 %) on mangrove forests (Fig. 1).

Warming and atmospheric CO_2 concentration were the only investigated drivers that had a positive effect on the growth rate of a mangrove *Avicennia germinans* (McKee and Rooth, 2008; Chapman et al., 2021; Akaji et al., 2019), although the overall effect remains mixed, unlike the overall effect of warming on metabolism classified as positive (Akaji et al., 2019). The effects of cooling, however, negatively impact all aspects of mangrove forests, such as habitat structure, metabolism, and photosynthesis, with a mixed overall effect on density/abundance (Cavanaugh et al., 2015; Osland et al., 2017; Krauss et al., 2008). Rooting gets inhibited below 15 °C and above 37 °C for *A. germinans* and *Rhizophora mangle* (Krauss et al., 2008). Photosynthesis will cease if leaf temperature climbs to 38–40 °C (McKee et al., 2012), and photo-inactivation generally occurs below −6.1 °C, −5.3 °C, and −3.7 °C for *A. germinans*, *R. mangle* and *Laguncularia racemosa*, respectively (Cavanaugh et al., 2015).

Sea level rise affects mangrove distribution, causing shoreline retreat and mangrove forest degradation (Cohen et al., 2021). However, understanding the ability of mangrove forests to cope with sea level rise is difficult given the multiple factors in the equation (e.g., rooting expansion, sediment accretion, subsidence, sea level rise). Half of the studies on sea level rise focused on sediment accretion rate or vertical growth. Increased sediment inputs may promote forest expansion in some cases (Cohen et al., 2021), but the interaction of sedimentation with sea level rise remains complex and unclear (Xie et al., 2020). Two studies (McKee, 2011; Koch et al., 2015) attempted to assess thresholds in the rate of sea level rise, and these were site-specific. Koch et al. (2015) estimated that above 3 mm year^{-1} of sea level rise, mangrove forests would be lost in the Everglades with varying degrees of tolerance according to the type of mangroves (fringe, dwarf, scrub).

Reduced rainfall generally tends to lessen the growth rate of *Avicennia marina*, *R. mangle* and *L. racemosa* (Bompy et al., 2014). Mangrove forests have adapted to survive in a saline environment with species-specific tolerances. However, drought episodes can lead to hypersaline conditions, which increase *R. mangle* propagule mortality. Krauss et al. (2008) state that salinity ranging between 0 and 57 PSU is optimal for rooting success. Under hypersaline conditions of 60 PSU and above, Devaney et al. (2021) observed a 100 % mortality of propagules for *R. mangle*. The global-scale threshold of mean annual precipitation is 0.78 m, below which mangrove forests abundance strongly decreases (Osland et al., 2017; Gabler et al., 2017).

Extreme weather events can profoundly affect habitat structure, often increasing the number of dead and decaying trees (Walcker et al., 2019), reducing growth rate, and causing a lower leaf area index in

R. mangle and *A. germinans* (Feller et al., 2015). Studies show that *R. mangle* is much more sensitive than *A. germinans* with any damage to its tree structure, except for small branch breaks, associated with over 60 % mortality. Conversely, only significant damage, such as toppling or trunk break below breast height, caused mortality of *A. germinans* stems to rise by over 10 %. Imbert (2018) found that basal area loss increased significantly above 110–150 km h^{-1} for basin mangroves and above 178–209 km h^{-1} for fringe and scrub mangroves in east Caribbean mangrove forests.

Few articles examined the interactions between CC drivers and LS (Table 1, Fig. 2). Coastal development (2 % of mangrove studies), often combined with hydrologic disturbances (2 %) and nutrient enrichment (10 %), were the main threats reported as reducing mangrove forest resilience to the effects of CC. Nutrient inputs can increase the growth of scrub mangrove trees. Still, that benefit is offset by a decrease in their resilience to hurricane damage, potentially destabilising the system (Feller et al., 2015; Walcker et al., 2019). If undisturbed by LS, the reduced density of *R. mangle* trees following hurricanes can increase average diameter at breast height and aboveground biomass (Gulf of Mexico, Griffiths and Mitsch, 2021). Hayden and Granek (2015) showed that sediment elevation increased at intact mangrove plots but decreased at cleared mangrove plots. Attempts to increase sedimentation (for instance, from beach nourishment) were found to benefit mangrove forests temporarily (Cohen et al., 2021). Hughes et al. (2018) studied the response of *A. germinans* to oiling and found a greater reduction in survival when *A. germinans* grew alone (21 % reduction) rather than with *S. alterniflora* (12 % reduction) throughout the experiment. No threshold was reported relative to LS interacting with CC drivers.

3.1.3. Seagrass beds – Thalassia testudinum

Research efforts on the effect of CC on *T. testudinum* (9 articles) have mainly focused on hypersalinity (44 % of the studies) but also warming (22 %), extreme weather events (22 %) and sea level rise (11 %; Fig. 1).

Hypersalinity had a negative effect on plant growth rate (Koch et al., 2007c; Koch et al., 2007b), density/abundance (Koch et al., 2007c; Koch et al., 2007b) and photosynthesis (Koch et al., 2007c; Koch et al., 2007b; Howarth and Durako, 2013; Johnson et al., 2018; Fig. 1). *T. testudinum* was highly tolerant to hypersaline conditions up to a 60 PSU threshold level when salinity was slowly increased (1 PSU day^{-1}). However, pulsed salinity treatments, without a slow osmotic adjustment period, reduced threshold levels of salinity by 20 PSU to approximately 45 PSU (Koch et al., 2007c). Hypersalinity at 65 PSU seems to affect the oxidizing capacity of *T. testudinum* and places subtle demands on the positive oxygen balance in the ecosystem (Koch et al., 2007b).

Warming affects the spatial distribution of seagrass, specifically from long-term and acute heat stress (Carlson et al., 2018). Experimentally increased temperature reduced growth rate and photosynthesis efficiency (Koch et al., 2007a), although it did not affect biomass (Koch et al., 2007a). While plants survived 38 days of temperature treatments, there was a clear thermal threshold above 33 °C where *T. testudinum* growth declined, and leaf quantum efficiencies (F_v/F_m) fell below the lower "stress" threshold of 0.7 (Koch et al., 2007a).

Extreme weather events reduced cover, especially in exposed meadows (Hernández-Delgado et al., 2020; James et al., 2021). Most of the documented impacts of hurricanes were associated with sediment bedload (horizontal transport) and displacement of coral rubble, which resulted in plant burial and suffocation of *T. testudinum* (Hernández-Delgado et al., 2020; James et al., 2021).

Sea level rise had a negative impact on spatial distribution, with a predicted decline in cover of 20 % for every metre of sea level rise along the Florida Gulf Coast (McHenry et al., 2021). However, the exact impact of sea level rise on the distribution and total cover of a *T. testudinum* population seemed to depend heavily on the local context (e.g., the possibility of moving shoreward).

Very few articles looked at interactions between CC drivers and LS

(Fig. 2); however, Hernández-Delgado et al. (2020) found that a shift in vegetation cover triggered by hurricanes favours the invasion of invasive seagrass (i.e., *Halophila stipulacea*) over *T. testudinum* (Fig. 2). In addition, an increased oxygen demand and high sulfate reduction rates in sediments were suggested to explain the frequent die-off events in Florida Bay, particularly after periods of high temperature and salinity (Koch et al., 2007b). As such, it was hypothesized that the interaction between hypersalinity and sulfide toxicity in *T. testudinum* is their synergistic effect on the critical oxygen balance of the plant (Koch et al., 2007b; Johnson et al., 2018). The oxygen threshold for sulfide intrusion in *T. testudinum* was found to be 1.3 (at 35 PSU) to 1.5 kPa O_2 (at 65 PSU) in the meristem or 7–8 % of overlying water saturation with no significant difference in the salinity treatments (Johnson et al., 2018). Results also indicated that high temperatures (>33 °C), high salinity (>45 PSU) and organic loading-induced porewater sulfide stressors have the potential to disrupt carbon metabolism in *T. testudinum* (Koch et al., 2007a; Koch et al., 2007b).

3.2. Mediterranean

3.2.1. Coral – Cladocora caespitosa

In total 13 articles were analysed, of which warming is the most studied CC driver in *Cladocora caespitosa* coral beds and micro-reefs (88 %) (Fig. 3). Summer heatwaves have been impacting this coral since the beginning of the 2000s, triggering widespread and recurrent mass mortality events (Kersting et al., 2013; Garrabou et al., 2009). Although there are differences among regions, seawater temperature maintained over the 26 °C–28 °C threshold range has been reported to trigger warming-induced necrosis in this coral.

Experimental studies assessing the impact of acidification (12 % of the studies) show contrasting results. On one side, pH values projected for the end of the century caused a reduction of ~30 % in *C. caespitosa* calcification rates (Movilla et al., 2012). On the other side, Rodolfo-Metalpa et al. (2009) found that a similar decrease in pH, alone or in combination with warming, had no significant effect on photosynthesis and calcification.

Two studies (12 %) have shown interactive effects of CC and LS on *C. caespitosa* (Table 1, Fig. 4). Invasive algae could interact synergistically with warming, increasing mortality in this species (Kersting et al.,

Marine & Coastal Ecosystems **Mediterranean**	RESPONSE VARIABLE CATEGORIES	Warming / heat waves	Extreme weather events	Atmospheric CO_2 concentration	Ocean acidification	Sea level rise	Salinity (hyper)	Cooling	Rainfall regimes	Inundation
		CLIMATE CHANGE								
CORALS *Cladocora caespitosa*	Density/Abundance	45%								
	Distribution									
	Growth	18%			66%					
	Habitat structure									
	Metabolism	9%								
	Photosynthesis/Respiration	9%			33%					
	Reproduction	9%								
	Other	9%								
	Total number of studies	**11**			**3**					
SEAGRASS BEDS *Posidonia oceanica*	Density/Abundance	18%	100%		22%		8%			
	Distribution	5%				50%	8%			
	Growth	23%			11%		16%			
	Habitat structure	3%			11%	50%	15%			
	Metabolism	28%			22%		39%			
	Photosynthesis/Respiration	18%			22%		15%			
	Reproduction	5%								
	Other	3%			11%					
	Total number of studies	**40**	**2**		**9**	**2**	**13**			

Response Legend:
- Negative: Fully / Mostly
- Positive: Fully / Mostly
- Neutral: Fully / Mostly
- Unclear: Fully / Mostly
- Mixed
- Not tested

Fig. 3. Summary of studies per climate change drivers and general effects on broad response variable categories in marine and coastal ecosystems of the Mediterranean. Percentage values represent the proportion of studies per response variable from the total number of studies per CC driver, indicated in bold for each ecosystem. Mediterranean outputs on maërl beds and salt marshes are included in Fig. 5.
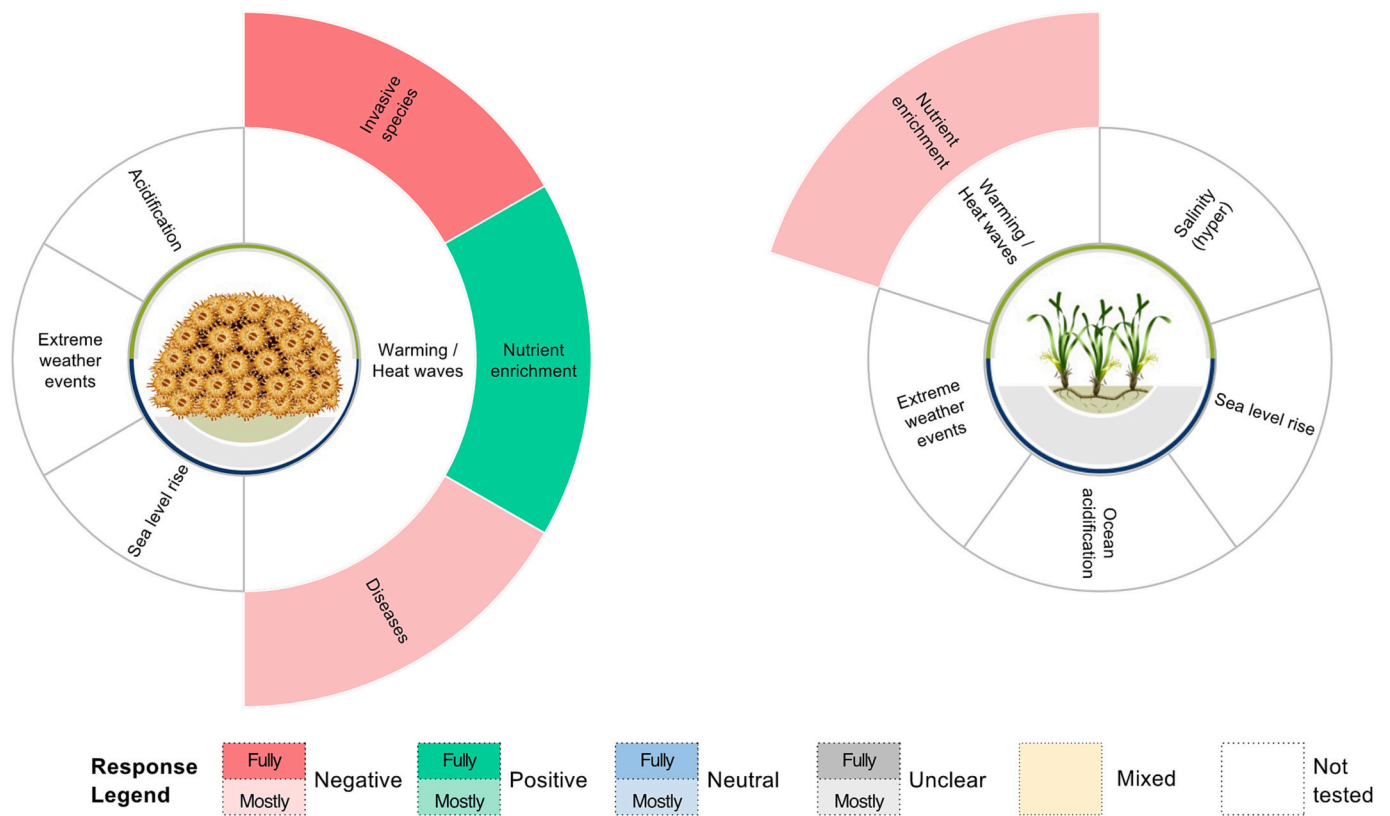
Fig. 4. Cumulative overall effects of local stressors combined with climate change drivers for marine and coastal ecosystems in the Mediterranean. Left: Coral (i.e. *Cladocora caespitosa*); right: Seagrass beds (i.e., *Posidonia oceanica*).

2015), and local nutrient enrichment could reduce the adverse effects of summer heatwaves on the corals (Hadjioannou et al., 2019).

Cladocora caespitosa shows highly parsimonious population dynamics (slow growth and low recruitment rates), which makes it highly vulnerable to catastrophic disturbances such as warming-related mortality events (Kersting et al., 2014b). However, recoveries from CC disturbances have also been reported for this species, showing a survival strategy that allows it to withstand and partially recover from thermal stress (Kersting and Linares, 2019).

3.2.2. Maërl beds

Only two articles focused on Mediterranean maërl beds, with acidification (50 %) and warming (50 %) as primary concerns. There is no empirical information on the effects of warming on maërl beds; however, it is expected to affect their extension due to their fragmented distribution ranges and poor dispersal capacity (Kružić, 2014).

Regarding acidification, field-based studies in the Mediterranean have identified the presence of maërl only a few metres away from hydrothermal vents, at a pH between 7.7 and 8.2; however, maërl was absent at pH below 7 (Linares et al., 2015). Experiments have observed that below optimal pH conditions 8.16–8.21, the maërl-forming species increase calcification rates to compensate for the adverse effects of the acidified environment until reaching a pH threshold at 7.7–7.9 (Kružić, 2014).

In terms of LS, trawling activities in the deep areas cause massive mortality of maërl by crushing and burying the rhodoliths (de Juan et al., 2013). Increased near-bottom turbidity caused by trawling also affects maërl beds due to light attenuation, identified in the global modelling study by Fragkopoulou et al. (2021).

In the shallower areas with higher light irradiance, maërl beds would be more affected by invasive algae species. At least three species are known to threaten these habitats in the Mediterranean: *Womersleyella setacea*, *Caulerpa racemosa* v. *cylindracea* and *Caulerpa taxifolia*. By

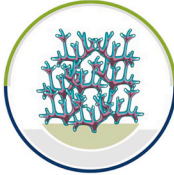covering the basal stratum, invasive algal species decrease rhodolith survival (Kružić, 2014).

3.2.3. Seagrass beds – Posidonia oceanica

The effects of CC drivers were principally negative on *P. oceanica* (25 articles), except for ocean acidification (8 % of the studies), which generally has a neutral impact (Fig. 3), probably due to the pH buffering capacity of Posidonia (Cox et al., 2016).

Warming (68 % of studies) was reported to have a negative impact due to enhanced mortality (Marbà and Duarte, 2009; Guerrero-Meseguer et al., 2017; Hernán et al., 2017; Pazzaglia et al., 2020), reduced growth rate (Olsen et al., 2012; Guerrero-Meseguer et al., 2017; Ruiz et al., 2018; Marín-Guirao et al., 2018; Traboni et al., 2018; Marín-Guirao et al., 2019; Ruocco et al., 2019), reduced distribution (Chefaoui et al., 2018; Papaki et al., 2020), and increased grazing rate (Hernán et al., 2017). Temperature above 27 °C has been found to limit the growth of *P. oceanica* (Guerrero-Meseguer et al., 2017; Ruiz et al., 2018). If the water temperature increases by 15 %, more than half of *P. oceanica* meadows may be replaced by *Cymodocea nodosa* (Papaki et al., 2020). The negative effect of warming was also observed at the physiological level by modifying the carbon balance (Hernán et al., 2017; Marín-Guirao et al., 2018) and photosynthesis/respiration rates (Marín-Guirao et al., 2016; Guerrero-Meseguer et al., 2017; Marín-Guirao et al., 2018; Ruocco et al., 2019; Nguyen et al., 2021). Nevertheless, the physiological resistance to warming seems to vary with depth, latitudinal range, and level of eutrophication. Plants in deeper areas experience higher heat-induced photosynthetic injury and impaired carbon balance (Marín-Guirao et al., 2016; Marín-Guirao et al., 2017a; Tutar et al., 2017); plants in more eutrophic waters show reduced physiological resistance to warming (see Fig. 4, Pazzaglia et al., 2020); and populations adapted to colder waters accumulated significantly more fatty acids following heat stress than the ones adapted to warmer waters (Beca-Carretero et al., 2018; Marín-Guirao et al., 2019). However, most

studies that investigated the effect of warming on metabolism in *P. oceanica* could not determine whether the response was negative, positive or neutral at the ecosystem, population or individual level. As such, the overall effect of warming on metabolism in *P. oceanica* was considered unclear.

Hypersalinity (16 %) has a negative impact on habitat structure (Ruiz et al., 2009; Marín-Guirao et al., 2017b) and distribution (Houngnandan et al., 2019), while no effect was found on photosynthesis or respiration (Marín-Guirao et al., 2013; Marín-Guirao et al., 2017b). Hypersalinity also has negative effects on metabolism: a

Marine & Coastal Ecosystems North-East Atlantic	RESPONSE VARIABLE CATEGORIES	CLIMATE CHANGE								
		Warming / heat waves	Extreme weather events	Atmospheric CO_2 concentration	Ocean acidification	Sea level rise	Salinity (hypo)	Cooling	Rainfall regimes (reduced)	Inundation
KELP FORESTS	Density/Abundance	9%								
	Distribution	23%					58%			
	Growth	20%					8%			
	Habitat structure	2%	100%							
	Metabolism	16%								
	Photosynthesis/Respiration	17%					17%			
	Reproduction	13%					17%			
	Other									
	Total number of studies	179	1				12			
MAËRL BEDS	Density/Abundance									
	Distribution	33%			9%					
	Growth	33%			36%					
	Habitat structure									
	Metabolism	33%			27%					
	Photosynthesis/Respiration				27%					
	Reproduction									
	Other									
	Total number of studies	4			13					
SALT MARSHES	Density/Abundance	3%		7%		7%			6%	
	Distribution									
	Growth	16%		21%		12%				
	Habitat structure	32%		14%		52%			69%	
	Metabolism					5%			19%	
	Photosynthesis/Respiration	41%		29%		15%			6%	
	Reproduction	8%		21%		8%				
	Other		100%	7%		2%				
	Total number of studies	37	1	14		60			16	
SEAGRASS BEDS *Zostera marina*	Density/Abundance	18%					15%			
	Distribution	3%	100%				8%			
	Growth	15%					15%			
	Habitat structure	9%					15%			
	Metabolism	42%					38%			
	Photosynthesis/Respiration	12%					8%			
	Reproduction									
	Other									
	Total number of studies	33	1				13			

Response Legend: Fully / Mostly Negative; Fully / Mostly Positive; Fully / Mostly Neutral; Fully / Mostly Unclear; Mixed; Not tested
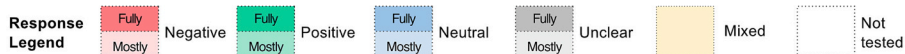
Fig. 5. Summary of studies per CC drivers and general effects on broad response variable categories in marine and coastal ecosystems of the North-East Atlantic. For maërl beds, articles from the Mediterranean (2) and North Atlantic (9) are merged due to the low number of articles. For salt marshes, the four articles (39 studies) covering the Mediterranean were also included, considering they studied genus and/or species found in the North-East Atlantic and were thus deemed relevant for our analysis. Percentage values represent the proportion of studies per response variable from the total number of studies per CC driver, indicated in bold for each ecosystem.

negative effect on rhizome non-structural carbohydrate content (Ruiz et al., 2009) and leaf pigment content (Marín-Guirao et al., 2013), and a positive effect on necrotic leaf area (Ruiz et al., 2009). However, some studies reported no effect on non-photochemical quenching (NPQ) and level of xanthophyll de-epoxidation (Marín-Guirao et al., 2013) or mixed effects on metabolism (Marín-Guirao et al., 2017b). The impact of hypersalinity is not considered to be driven by CC but instead was attributed to LS, such as hypersaline effluents from desalinisation plants or coastal lagoons (Ruiz et al., 2009; Marín-Guirao et al., 2017b). Salinity tolerance was identified to be 38 PSU, which is close to the mean salinity in the Mediterranean Sea (Ruiz et al., 2009). However, *P. oceanica* meadows experiencing long-term salinity fluctuation show adaptive capacity by reducing shoot size (Marín-Guirao et al., 2017b).

Increased sedimentation due to extreme weather events (4 %) can be detrimental to *P. oceanica*, for which 4–5 cm of sedimentation starts to induce shoot mortality with near-complete mortality at a burial level of 8–9 cm (Gera et al., 2014).

Sea level rise (4 %) was suggested to have a negative impact on distribution and habitat structure. This negative effect was attributed to an attenuation of the amount of light at the seabed, reducing photosynthetic activity in *P. oceanica*, which eventually can cause mortality, especially in meadows at the lower limit (Pergent et al., 2015).

Only one study by Pazzaglia et al. (2020) tested for interactive effects between CC stressors and LS on various response variables in *P. oceanica* plants collected from populations from two environments with different nutrient load history (i.e., growing under chronic cultural eutrophication or growing in oligotrophic pristine waters). Plants experiencing chronic cultural eutrophication were more sensitive to further exposure to multiple stressors than plants growing in oligotrophic habitats and appeared to be weaker during the treatments, showing the highest mortality rate, especially under increased temperature (Pazzaglia et al., 2020).

3.3. North-East Atlantic

3.3.1. Kelp forests

All reviewed articles (34 articles) had warming as their main CC driver, from which 35 % of the studies had heatwaves, 15 % had salinity, and 6 % had storms (Fig. 5). Most studies corresponded to laboratory or modelling experiments where a response variable changed depending on a limited number of established conditions (often one or two variables).

Temperature threshold values that differ between sporophyte and gametophyte have been defined for several kelp species. For example, in *Laminaria digitata* and *Laminaria hyperborea*, the sporophyte dies at temperatures higher than 23 °C (Derrien-Courtel et al., 2013; Liesner et al., 2020) while the gametophytes of both species show different thermal behaviour. Gametophytes of *L. digitata* can tolerate temperatures around 25 °C (Martins et al., 2020), while gametophytes of *L. hyperborea* have a maximum temperature of 18 °C for growth and reproduction (Derrien-Courtel et al., 2013). *Laminaria ochroleuca,* with southern distribution limits, presents a higher tolerance to temperature with threshold values of 25 °C for gametophyte and sporophyte (Derrien-Courtel et al., 2013). The warming temperature may change the distribution of some species, as seen along the Cantabrian coast of Spain (Díez et al., 2012). Here two species, *Saccorhiza polyschides* and *L. ochroleuca* were lost entirely from 1991 to 2008, whereas Araújo et al. (2016) showed that the same two species had an unchanged presence on the Galician coast of Spain and in north Portugal. Warming may also alter the species' dominance, where the warm-water species *L. ochroleuca* takes over the cold-water species *L. hyperborea* (Teagle et al., 2018). Thermal stress might trigger a shift from a kelp forest to a turf community (Filbee-Dexter et al., 2016; Filbee-Dexter and Wernberg, 2018; Feehan et al., 2019), and as turf communities trap sediments, such a shift prevents kelp from re-establishing (Feehan et al., 2019). There are additional suggested drivers for this change, like eutrophication leading

to epiphytism, pollution and storms (Filbee-Dexter and Wernberg, 2018). Warming and radiation, as well as their interaction, can alter the physiological processes of kelp, such as photosynthesis (Fredersdorf et al., 2009; Pereira et al., 2015; Hargrave et al., 2017) or metabolism (Müller et al., 2012; Olischläger and Wiencke, 2013). In Arctic regions, ice-thickness, which is tightly linked to warming, was also found to influence the distribution of kelp due to its influence in the light regimes (Assis et al., 2018; Assis et al., 2016).

Regarding the effects of salinity, sporophytes of *Alaria esculenta* showed minor effects of decreased salinity, while zoospores were more sensitive (Fredersdorf et al., 2009). Only a few studies reported threshold values for salinity. For example, Fredersdorf et al. (2009) found that a salinity below 5 PSU affects the photosynthesis of *A. esculenta*. In comparison, Assis et al. (2018) observed that salinity values lower than 7.9 PSU trigger bleaching and stop the growth in *L. hyperborea*. According to Franco et al. (2018), the golden kelp (*L. ochroleuca*) will not enter the Baltic Sea (PSU < 15), even if the temperature changes.

Extreme weather events have also been considered through models or experiments that simulate the storm effects, but no studies looked at the state of kelp populations before and after real storms. These modelled experiments report negative effects, including a severe reduction in invertebrate and fish populations after mechanical stress, like the physical removal of kelp (Norderhaug et al., 2020).

Most studies considering the interaction of CC and LS focused on *Saccharina latissima*. The LS were physical stress such as grazing (8 %), followed by nutrient enrichment and eutrophication (3 %) and sedimentation (3 %) (Table 1, Fig. 6). Grazing has been found to negatively affect kelp populations in most cases (O'Brien and Scheibling, 2018), except for grazing on turf communities. Under certain conditions, grazing may have positive effects that counteract the negative effects of sedimentation. For example, after laboratory experiments, Zacher et al. (2016) reported that with 1 g of sediment cover, sporophytes of *S. latissima* only developed when grazers were present (sediment removal). Nutrient enrichment, including eutrophication, generally negatively affects kelp populations; however, the magnitude of these effects is species-specific. While Moy and Christie (2012) reported eutrophication to have a negative effect on the abundance of *S. latissima*, Martins et al. (2017) did not find any significant effect of nutrient enrichment or its interaction with temperature on the life stage transitions of *Laminaria digitata*. The physical stress included a variety of factors that can produce different effects on kelp populations. The ones resulting from fishing activities (i.e. kelp trawling), which are analogous to the effects of extreme weather events, negatively affected kelp and its associated populations. For example, Norderhaug et al. (2020) conducted experiments of kelp trawling on *L. hyperborea* populations and reported a reduction of 67 % in epiphytes and 87 % in invertebrate populations.

3.3.2. Maërl beds

The review identified nine articles on North-East Atlantic maërl beds and two global articles on warming (Cornwall et al., 2019) and trawling effects on maërl (Fragkopoulou et al., 2021) for a total of 22 studies.

Ocean acidification (82 % of the studies) generally alters the metabolism of maërl-forming species (e.g., Burdett et al., 2012; Sordo et al., 2018) and reduces their calcification rates (e.g., Donald et al., 2017; Legrand et al., 2017; Burdett et al., 2018) although it remains a mixed result due to neutral and unclear effects (Fig. 5). Similar to Mediterranean studies, Donald et al. (2017) suggests that for *Neogoniolithon* sp., the optimal pH is 8, and the limit is 7.5. Ocean acidification might also negatively affect grazers (e.g., gastropods, sea urchins) and thus decreasing their control on epiphytes growth over maërl beds, which has negative consequences on rhodolith photosynthesis (Legrand et al., 2017).

Warming is causing negative effects on the calcification (referred to as growth in Fig. 5) of maërl-forming species (e.g., Cornwall et al.,
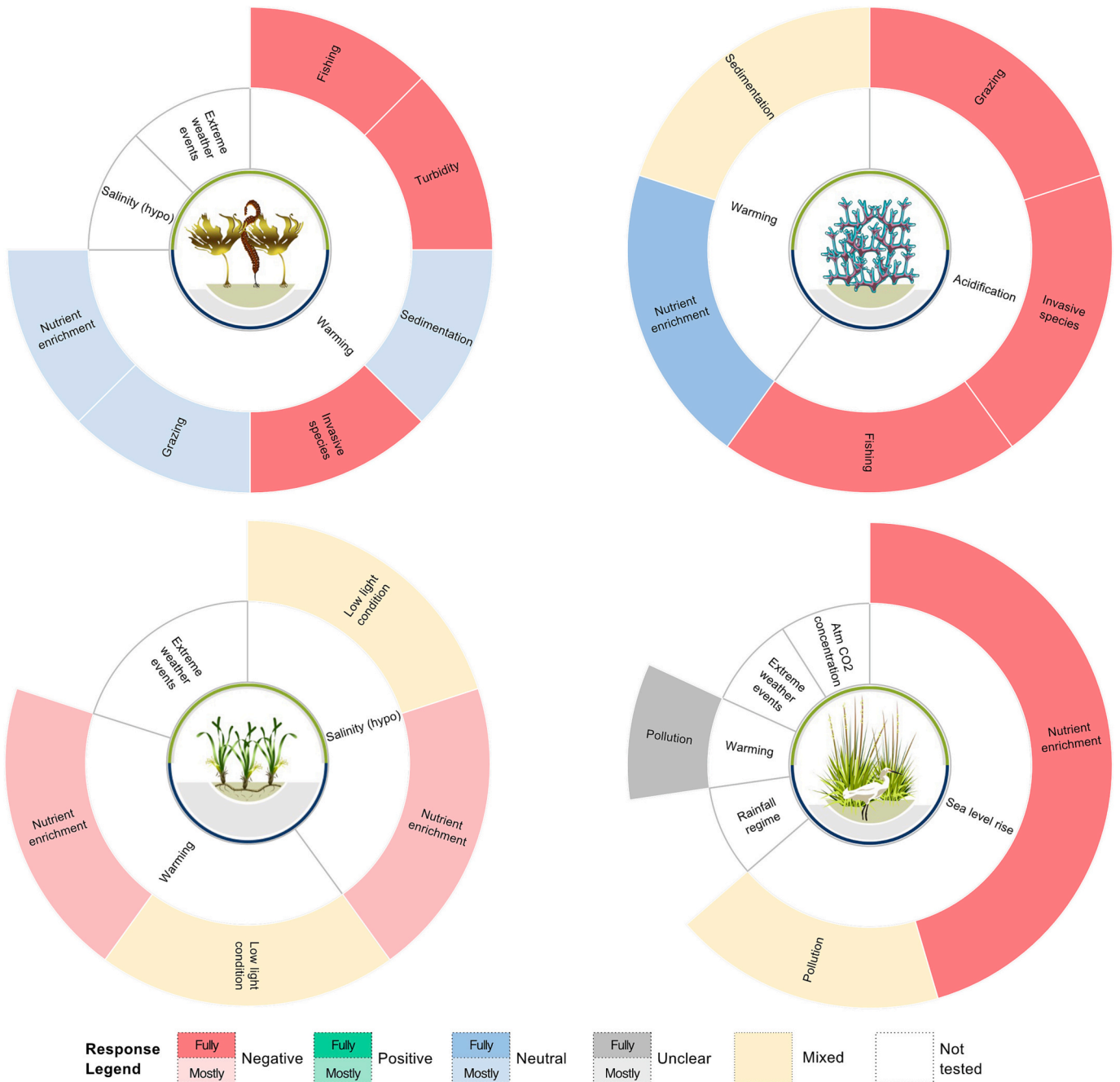
Fig. 6. Cumulative overall effects of local stressors combined with climate change drivers for marine and coastal ecosystems in the North-East Atlantic. Top left: kelp forests; top right: maërl beds; bottom left: seagrass beds (i.e., *Zostera marina*); bottom right: salt marshes.

2019). Higher latitudes are expected to be the refuge for maërl beds in the North-East Atlantic due to the lower temperatures (Simon-Nutbrown et al., 2020). However, while one study by Cornwall et al. (2019) observed that a 5.23 °C increase above baseline temperature decreases calcification, there is limited knowledge of the temperature tolerance for maërl-forming species. One species (*Lithothamnium coralloides*) is reported to have a higher affinity for low temperatures (Qui-Minet et al., 2019); however, for temperature, pH, or light availability, the limiting thresholds would probably differ between rhodolith species (Fragkopoulou et al., 2021), with species-specific responses.

A combined effect of warming and ocean acidification implies that under all RCPs, a significant decrease in suitable habitat for maërl beds is predicted, with at least a 38 % decline by 2050, down to 83,7 % in 2100 under RCP 8.5 (Simon-Nutbrown et al., 2020).

Other interactions with LS involve fishing activities, invasive species and sedimentation (Fig. 6). On top of the direct physical impact of bottom trawling, increased near-bottom turbidity caused by trawling affects maërl beds distributed nearby fishing areas due to light attenuation, which causes additional losses of rhodoliths (Fragkopoulou et al., 2021). Few studies provide empirical evidence on the effects of increased sediment input on maërl survival. In the case of *Lithothamnion* sp. in the Bay of Brest (Brittany), the death of the rhodoliths occurs after 41 days of being buried by sediment (Ehrhold et al., 2021).

3.3.3. Salt marshes

While there is extensive literature on the effects of CC stressors on salt marshes, only 25 relevant articles were found for the European area, with 128 studies extracted. Four articles focus on the Mediterranean,

with genus and/or species also found in the North-East Atlantic and therefore deemed relevant for our analysis here. Sea level rise (47 % of the studies) and warming (29 %) were the main CC drivers affecting salt marshes. However, the effects of rainfall regime (13 %), atmospheric CO_2 concentration (11 %) and extreme weather events (1 %) were also studied to a lesser extent (Fig. 5). It is worth noticing that the effects of these stressors were highly mixed due to the different species' responses in these often highly diverse environmental settings.

The effects of increased temperature on salt marshes were mixed, with some studies reporting a decrease in salt marshes' extent area and the growth of some species (Duarte et al., 2021; Mateos-Naranjo et al., 2021), while other studies reported increase in extent areas, growth (Duarte et al., 2021; Bitoun et al., 2018; Gray and Mogg, 2001), and biomass, therefore contributing to carbon sequestration (Couto et al., 2014; Gray and Mogg, 2001; Strain et al., 2017). Interestingly, increased temperatures also led to opposite responses in the photosynthetic efficiency of the plants depending on species studied in the same region (Duarte et al., 2016; Carreiras et al., 2020; Duarte et al., 2021), but also for the same species (*Halimione portulacoides*) studied twice in the same region (Carreiras et al., 2020; Duarte et al., 2021).

Increased salinity associated with sea-level rise would lead to a community shift from species with stiff stems to species with more flexible stems, characteristics of pioneer/low marsh communities (Zhu et al., 2020b). Boorman (1992) further found that increasing sea level rise, combined to some extent with coastal development, would lead to a progressive loss of marsh zones with only pioneer/low marsh communities remaining at the highest level of sea level rise. Whether in the North-East Atlantic or the Mediterranean, studies found that sea level rise would overall negatively affect salt marshes' extent area (Boorman, 1992; Duarte et al., 2021) and biomass (Strain et al., 2017; González-Orenga et al., 2020; Brown et al., 2006; Wong et al., 2015; Reents et al., 2021), but also their growth (Duarte et al., 2021), survival and abundance (Castillo et al., 2000; Duarte et al., 2021; Brown et al., 2006), and reproduction (Szymansky et al., 2021; Zhu et al., 2020a; Mesa-Marín et al., 2019).

Only five articles have identified thresholds or tipping points for salt marshes, all related to sea level rise. Some studies in the Mediterranean looked at the effect of the inundation period related to the mean sea level, for which a 37.5 % period (and above) relating to a decrease of 5 cm below the current mean sea level could lead to a die-off of *Spartina veneta* (Strain et al., 2017). *Spartina* spp. showed a higher tolerance with a threshold at 73 % of the inundation period corresponding to a 10 cm rise above the current mean sea level (Strain et al., 2017). Other studies in the North-East Atlantic looked at the sea level rise threshold itself, varying from 0.5 m to 1.5 m, with successive mortality from high to low marshes plants (Boorman, 1992; Castillo et al., 2000). Furthermore, besides the increase in inundation period, the wave-imposed sheer water stress on the tidal flat associated with sea level rise could significantly affect the reproduction of *Spartina anglica*, with <10 % of seed retention from a threshold of 0.022 Pa and above (Zhu et al., 2020a). Finally, sea level rise could also significantly affect the reproduction of *Salicornia ramosissima* through the associated increased salinity, considering no germination was observed above a 1030 mM NaCl threshold under laboratory conditions (Mesa-Marín et al., 2019).

Nine articles looked at LS, which were coastal development, dredging, grazing, invasive species, nutrient enrichment, pollution, and sedimentation, but only two of them looked at the interactions between CC drivers and LS, and both focused on heavy metal pollution (Table 1, Fig. 6). Indeed, in the Tagus estuary, Portugal, *Spartina patens* and *Halimione portulacoides* from heavy metal contaminated areas seemed more resilient and tolerant to salt stress resulting from sea level rise and more resistant to heat stress, respectively, than the same species from pristine areas. However, the underlying mechanisms remain unclear (Carreiras et al., 2020; Carreiras et al., 2021). Finally, while the interaction is not formally tested, coastal development would hamper salt marshes' ability to cope with sea level rise by preventing their landward

migration even where their accretion rate would be sufficient to keep up with sea level rise (Boorman, 1992), a phenomenon better known as "coastal squeeze" (e.g., Doody, 2013).

3.3.4. Seagrass beds – Zostera marina

Out of the 14 articles, the major CC stressor studied for *Z. marina* is warming (72 % of the studies), which has a negative effect on density and abundance (Holmer and Bondgaard, 2001; Ehlers et al., 2008; Bergmann et al., 2010; Salo and Pedersen, 2014; Franssen et al., 2014; Moreno-Marín et al., 2018), rates of photosynthesis (Holmer and Bondgaard, 2001; Winters et al., 2011; Mota et al., 2018), habitat structure (Holmer and Bondgaard, 2001; Ehlers et al., 2008; Salo and Pedersen, 2014), distributional range (Torn et al., 2020), and growth (Holmer and Bondgaard, 2001; Salo and Pedersen, 2014; Moreno-Marín et al., 2018), although some studies found no effect of warming on growth (Bergmann et al., 2010; Salo and Pedersen, 2014). Looking at the metabolism, warming was reported to decrease the non-structural carbohydrate reserves in roots (Holmer and Bondgaard, 2001) and leaves (Moreno-Marín et al., 2018), increased heat-shock-protein up-regulation which indicated molecular stress (Franssen et al., 2011; Franssen et al., 2014; Jueterbock et al., 2016), and increased toxic sulfide intrusion (Pedersen et al., 2004). In contrast, warming was reported to reduce the abundance of the pathogen *Labyrinthula zosterae* in *Z. marina* tissues (i.e. wasting disease; Brakel et al., 2019). Overall, a temperature above 25 °C had a negative impact on *Z. marina*'s survival (Moreno-Marín et al., 2018).

Hyposalinity was reported to have a negative effect on the distributional range (Torn et al., 2020), density and abundance, growth, habitat structure and metabolism (Salo and Pedersen, 2014; Villazán et al., 2015), necrotic lesion coverage due to infection with *L. zosterae* (i.e., wasting disease; Brakel et al., 2019) and carbon balance through increased respiration rates (Villazán et al., 2015). Below 12.5 PSU, the growth of *Z. marina* decreases, and mortality increases (Villazán et al., 2015).

Only three articles investigated the effects of CC-drivers combined with LS on *Z. marina* performance (Fig. 6). Experimental work by Villazán et al. (2015) showed that increased ammonium availability, which is considered a LS (nutrient enrichment), amplified the adverse effect of low salinity on growth-related variables and survival. In addition, Moreno-Marín et al. (2018) showed that individual exposure to either heat or shade had a negative effect on *Z. marina* performance, which, to some extent, was also the case for the effect of high nitrogen availability. While the combined effects of these stressors were additive, a synergistic effect on mortality was found for *Z. marina* plants exposed to all three stressors simultaneously (Moreno-Marín et al., 2018). Finally, Brakel et al. (2019) found that light conditions had no interactive effects with elevated temperatures on the physiological resistance of *Z. marina* to infection by the pathogen *L. zosterae*, nor on a cluster of *Z. marina* fitness variables (i.e., leaf growth rate, shoot survival, leaf sucrose content). They also found that light conditions did not alter the negative effect of reduced salinity on necrotic lesion coverage (%) 2 days after inoculation with *L. zosterae*. Interestingly, Brakel et al. (2019) did find a negative synergistic interaction between high temperatures and low salinity on the abundance of the pathogen *L. zosterae* within leaf tissue, preventing wasting disease symptoms.

4. Discussion

4.1. Drivers of change of marine coastal ecosystems in the Caribbean ecoregion

The Caribbean coastal and marine ecosystems are threatened by sea level rise, warming, stronger hurricanes, and drier conditions, with coral reefs, mangroves, and seagrass particularly vulnerable (Beckford and Rhiney, 2016; Rull, 2022).

Sea level rise and ocean acidification are mostly a concern for

mangrove forests and coral reefs, respectively. The pace at which mangroves can cope with sea level rise is highly dependent on the geomorphology and the net balance between sedimentation and erosion. As such, understanding the mechanisms that determine sediment accretion rate is crucial to assessing the adaptive capacity of mangrove forests to sea level rise. Even though the impacts of ocean acidification on coral calcification rates are mostly negative and species dependent, they remain, in many cases, not severe. The severity of marine heat waves is, however, of primary concern for coral reefs as these events can decimate coral populations through bleaching and associated mortality, leading to communities dominated by thermal-resistant species (Smith et al., 2013) or dominated by algae (McCook et al., 2001) if the reef is under the influence of local stressors such as increased nutrient inputs, which further favour algae dominance over corals (Lapointe, 1997). The combination of warming and nutrient enrichment also favours the prevalence of coral diseases (Randall and van Woesik, 2015; Randazzo-Eisemann et al., 2022). Based on models trained with environmental data from the Caribbean/Atlantic, global coral reef loss by 2100 is predicted to be 83 % for Representative Concentration Pathway (RCP) RCP4.5 and 88 % for RCP8.5 (Freeman et al., 2013). Tropical seagrass beds dominated by native *T. testudinum* might suffer from rapid, large-scale die-off events from the combination of high temperatures, high salinity and the interactive stressor sulfide (Koch et al., 2007a; Koch et al., 2007b; Johnson et al., 2018). Mangrove forests are also highly vulnerable hypersaline conditions due to drought episodes resulting from warming and longer dry seasons.

In the context of coral mortality and acidification, calcification rates decrease, vertical growth cannot keep up with sea level rise, and the reef is flattening from bioerosion and continues its shift to weedy species. With a flattened reef, the services provided by the reef are strongly affected, and the risk of coastal hazards from the combination of sea level rise and extreme weather events is a concern for coastal communities, including associated ecosystems. The increase in their intensity and frequency threatens all MCEs, especially if the recovery period between two successive events is not sufficient. In this case, opportunistic (invasive) or more resilient species might dominate during recovery (Snedaker et al., 1992). If coral reefs' ability to attenuate wave energy decreases, seagrass and mangrove forests could attenuate the remaining waves' energy and still protect the coast during extreme weather events, but higher hydrodynamics on the long term is not ideal for the settlement of mangrove trees. Short-term and long-term CC impacts, therefore, depend heavily on the local context of MCEs (e.g., exposure, presence of invasive species, and local stressors). Since the invasive seagrass species *Halophila stipulacea* has spread across most of the Eastern Caribbean islands (Winters et al., 2020), extreme weather events might facilitate the shift from native to invasive vegetation. The combined effects could have significant consequences on seagrass ecosystem resilience and on the ability of the native seagrass species *T. testudinum* to persist and adapt to projected climate change impacts (Hernández-Delgado et al., 2020).

4.1.1. Management recommendations for the Caribbean ecoregion

4.1.1.1. Towards a watershed approach to coastal ecosystems conservation.
Due to tropical coastal ecosystems' intrinsic complexity and spatial variability, management cannot be designed using a "one size fits all" approach. Instead, local dynamics and stressors must be carefully considered (Blackwood et al., 2018). Reducing land-based local stressors from the catchment areas will increase MCEs resilience to CC (e.g., reduced nutrient input increased resilience to hurricanes in mangrove forests, see Walcker et al., 2019) and, in turn, contribute to mitigating its effects through the regulating services they provide (e.g., climate regulation and coastal protection). Therefore, a watershed approach to coastal ecosystem conservation is fundamental to reducing the impact of LS and allowing these ecosystems to adapt naturally to climate change.

Moreover, extreme weather events generally accentuate the negative effects of human alterations on the coastal environment and adjacent catchment areas, which increase sedimentation, turbidity and inputs of land-based nutrients and pollutants from terrestrial run-offs, translating into negative effects on coral reef benthic communities (Przeslawski et al., 2008; Otaño-Cruz et al., 2019) and associated ecosystems. For example, land clearing (if not directly mangrove forests) tends to increase turbidity and sedimentation, while agriculture (e.g., sugar cane) and poor water treatment facilities will strongly increase nutrient load in the coastal environment. These will strongly affect community structure on coral reefs, with the overgrowth of macroalgae (Pandolfi and Jackson, 2006) and survival of seagrass beds through eutrophication and light-limitation-induced sulfide stress (Johnson et al., 2018). Limiting land clearing and soil artificialisation, increasing wastewater treatment capacity, and reducing the use of fertilisers are just a few directions that could benefit MCEs greatly and sustain the service they provide to coastal communities.

4.1.1.2. Consider the connectivity between MCEs.
The interconnectivity of coral reefs, seagrass beds and mangrove forests implies that managing a local stressor specifically for coral reefs will indirectly benefit mangrove forests and seagrass beds, and vice versa. For instance, managing fisheries, mainly to protect herbivorous species, can reduce reef degradation associated with warming and extreme events (Mumby et al., 2014; Edwards et al., 2011) by preventing macroalgal growth and promoting the recovery in coral cover and density (Bozec et al., 2016; Steneck et al., 2019). Healthy reefs provide sheltered conditions for seagrass and mangrove to develop, providing additional coastal protection against extreme weather events and sea level rise. Managing mangroves and seagrass beds can benefit fish populations as they provide shelter and food for juveniles and adults. It will also significantly improve the water quality by absorbing excess nutrients and trapping sediment, all having cascading benefits on coral reefs (Barbier et al., 2011; Lamb et al., 2017). Mangroves can also act as light refuges and mediate coral bleaching and survival during marine heat waves (Stewart et al., 2021), just like upwelling areas in the Caribbean that have a particular conservation value because of lower rates of thermal warming (Chollett and Mumby, 2013).

4.1.1.3. Promote community-based ecological restoration actions.
Working with nature to consider MCEs ecology and biology to restore degraded MCEs by mimicking natural processes is necessary. For instance, any climate change driver or hydrologic disturbances that might lead to hypersaline conditions will significantly affect mangrove forests' structure, distribution, and productivity (Yoshikai et al., 2022). These changing conditions might alter the structure of the mangrove forests, going from tall mangrove forests to shrub mangroves and dead mudflat zones. del Mar Delgado-Serrano et al. (2017) provide a portfolio of successful cases of community-based management of environmental challenges in Latin America and the Caribbean. More recently, an excellent example of community-based ecological mangrove restoration can be found in Bonaire, in the Caribbean, aiming at maintaining and restoring the channels to restore water flow between the front and back of the mangroves in order to prevent the harmful effects of hypersalinity (van Zee, 2022). If successful, this initiative will give a chance to mangrove trees to thrive and be more resilient to CC.

4.2. Drivers of change of MCEs in the Mediterranean ecoregion

The Mediterranean is a climate change hotspot, and the sea surface temperature increase rate is 3 to 4 times higher than in the global ocean (Juza and Tintoré, 2021). Since the beginning of the 2000s, the Mediterranean Sea has been impacted by recurrent marine heat waves (Garrabou et al., 2009; Kersting et al., 2013; Marbà et al., 2015), whose intensity has significantly increased during the last years threatening

ecosystems' condition and functioning (Garrabou et al., 2022). Against this background, most of the studies on the impact of warming on Mediterranean benthic organisms started after the widespread mass mortality event of 2003 in the North-West Mediterranean Sea (Garrabou et al., 2009; Kersting et al., 2013).

Mediterranean shallow zooxanthellate corals (*C. caespitosa*) are among the benthic organisms most impacted by warming (Garrabou et al., 2009; Kersting et al., 2013), and future predictions will most likely increase the already worrying mortalities. Nevertheless, despite their vulnerability to increased temperatures, it has been found that these corals own specific mechanisms that could improve their long-term resilience to warming, like the long-term recovery processes described in warming-impacted *C. caespitosa* populations (Kersting and Linares, 2019). Likewise, in seagrass beds, a warming-induced flowering has been observed in *Posidonia oceanica*, which could be an adaptative strategy to increase the diversity of genetic and phenotypic responses to warming, escaping stressful temperature conditions, and potentially populating new areas (Ruiz et al., 2018; Marín-Guirao et al., 2019). However, *P. oceanica*-dominated seagrass beds could be replaced by *Cymodocea nodosa*-dominated seagrass beds if the water temperature increases significantly (Papaki et al., 2020). On the other hand, the deeper extension of maërl beds in the Mediterranean will most likely have a refuge function due to moderate increases in temperature and acidification at these depths, as long as they remain trawling-free (Fragkopoulou et al., 2021). In the shallower areas though, the higher irradiance might drive the proliferation of filamentous algae that overgrow on maërl beds when temperatures and nutrients load increase. Over 1000 non-indigenous species have been reported in the Mediterranean Sea (Zenetos et al., 2010, 2012), many originating from the Red Sea or the Atlantic, finding suitable environmental conditions as the Mediterranean Sea is getting warmer (Öztürk, 2021); invasive algae threaten key coastal ecosystems such as seagrass meadows (Klein and Verlaque, 2008) or coral beds (Kersting et al., 2014a).

Other significant effects include acidification, which is expected to drop by 0.4 unit by 2100, while the sea level is expected to rise between 0.43 and 2.5 m by 2100, depending on scenarios and projections (MedECC, 2020). Ocean acidification threatens mostly calcifying organisms such as the coral *C. caespitosa* and maërl. The fragmentation of the rhodoliths by the physical impact of trawling would probably accelerate de-calcification processes. The liberation of the carbon pools into CO_2 would further increase ocean acidification and atmospheric CO_2 emissions. Sea level rise will increase the risk of coastal flooding and storm surges and will likely affect the deep seagrass meadows at their lower limit. Mediterranean salt marshes might also suffer from sea level rise due to a combination of increased inundation period and salinity (Strain et al., 2017; González-Orenga et al., 2020).

In the Mediterranean, human-induced pressures such as coastal development, pollution, anchoring, fishing, and invasive species reduce the resilience of seagrass meadows, corals and maërl beds to CC drivers, increasing the risk of collapse by reaching a tipping point. Given that the reach of tipping points has already been evidenced after the recurrent heatwaves in summer over the past decade that caused impaired physiological and physical damage to *P. oceanica* meadows (Guerrero-Meseguer et al., 2017; Ruiz et al., 2018; Hernán et al., 2017) and mass mortality events since the beginning of the 2000s for the coral *C. caespitosa* (Kersting et al., 2013), environmental management actions must be reinforced.

4.2.1. Management recommendations for the Mediterranean ecoregion

4.2.1.1. Promote transnational actions. In the Mediterranean region, key management actions include regulating fishing activities over vulnerable habitats, a single action that is challenged by the large proportion of international waters in a region shared by many European and non-European countries (de Juan et al., 2012). The European Union has

implemented such regulations, prohibiting trawl fishing over Mediterranean coralligenous and maërl bottoms as specified in EC Regulation 1997/2006. In 2008, a Mediterranean-wide Action Plan for the Conservation of the Coralligenous and Other Calcareous Bio-concretions in the Mediterranean Sea was adopted under UN Environment/MAP. Furthermore, two common maërl-forming Mediterranean species, *Lithothamnion corallioides* and *Phymatolithon calcareum*, are covered by Annex V of the Habitats Directive. However, effective protection of maërl beds is hampered by limited published information on their actual presence, which challenges the implementation of protective measures.

Slowing the transit of non-indigenous species to the Mediterranean Sea through regional cooperation is another critical management action which should be prioritised and thoroughly investigated. Prevention, surveillance, citizen awareness raising, and control strategies should all be increased to prevent the introduction of alien species, detect their presence early and implement the right control measure. Furthermore, effectively protecting key species and habitats (Öztürk, 2021) makes them more resistant to invaders (i.e., biotic resistance hypothesis - Elton, 1958; Levine and D'Antonio, 1999).

An essential regional-level strategy involves the efficient implementation of marine protected areas networks that simultaneously monitor the impact of various management measures such as the reduction of destructive bottom-contact fishing nets, the implementation of invasive species monitoring program, and the stringent protection of highly sensitive species such as coral and *Cladocora*. However, implementing effective marine protected areas requires consensus or compromises among users (Costa et al., 2022) and nations, a challenge in the Mediterranean basin with multiple nations and policy frameworks (de Juan et al., 2012). But this is an important goal to achieve in the region as the connectivity between MCEs means they all benefit from each other.

4.2.1.2. Consider cumulative pressures. Henceforth, forthcoming protection measures and restoration programs must adopt a large-scale approach, exemplified by well-connected MPA networks, to effectively address the cumulative risks stemming from climate change-related and local stressors, which operate across various scales. The Mediterranean Sea is one of the basins where high coastal development and sea-based economies collide with ecological peculiarities requiring a careful conservation and management, so that a cumulative impact assessment can be particularly useful and recommendable. Between 60 and 99 % of the territorial waters of EU member states are subject to high cumulative impacts (Micheli et al., 2013). The paucity of quantified cumulative pressures and impacts assessment stresses the need for more incisive efforts to collect empirical evidence on ecosystem-specific responses to human pressure (Bevilacqua et al., 2018). As demonstrated by Pazzaglia et al. (2020), different nutrient loads impact *P. oceanica* physiological performance and morphological traits, highlighting the influence of local pressures in eliciting diverse adaptive strategies in response to global environmental changes, such as marine heatwaves that affect regional scales. With the predicted sea surface temperature increase, it has been suggested that *P. oceanica* would lose its functionality by reducing 90 % of its shoot density globally by 2049 (Jordà et al., 2012). While we need to be prepared for the loss of ecosystem services provided by *P. oceanica* meadows, we should also anticipate the loss of functionality of associated habitats due to collateral damages from the loss of *P. oceanica* meadows. This seascape approach extends its benefits to multiple key ecosystems. For instance, when conservation measures are implemented at the seascape level, seagrasses enhance water quality by efficiently filtering out pollution, pathogens, and nutrients, as demonstrated by Lamb et al. (2017). This, in turn, contributes to the well-being of associated habitats, including maërl beds and coralligenous habitats featuring *C. caespitosa*.

4.3. Drivers of change of marine coastal ecosystems in the North-East Atlantic ecoregion

In Northern Europe, temperatures will rise at a rate exceeding global mean temperature changes. The frequency and intensity of hot extremes, including marine heatwaves, are projected to continue increasing regardless of the greenhouse gas emissions scenario used. Extreme sea level rise events will become more frequent and more intense, leading to more coastal flooding, and severe windstorms are projected to increase at global warming of 2 °C and above (IPCC, 2022). Finally, pluvial flooding, attributed to human influence, is projected to increase further.

As seawater temperatures increase, scientists expect to see poleward expansions and contractions at lower latitudes of suitable habitats for kelp forests and maërl beds, with adverse effects on the associated biodiversity. For instance, assemblages associated with the cold-water species *Laminaria hyperborea* were on average > 12 times more diverse and supported >3600 times more biomass than the warm-water species *L. ochroleuca* because the latter has a stipe devoid of epibionts (Teagle et al., 2018). However, increased temperature could also have a positive effect on kelp forests. In northern Norway, increasing temperature along the coast allowed the southern population of crabs to move northwards, controlling sea urchins' grazing pressure on the kelp (Christie et al., 2019). Fagerli et al. (2013) found that increased temperature could reduce the sea urchins' fecundity, meaning less offspring, which benefits kelp forests. However, warming is also a driver for invasive species that could particularly influence the warmer shallow areas, generating competition for resources or a niche (Brodie et al., 2014). If ocean acidification and warming were to affect grazers' physiology (e.g., sea urchins), their control over epiphytes would decrease, resulting in negative consequences for maërl beds and potentially for kelp forests too.

The increased frequency and intensity of rainfall events result in many secondary effects such as increased pluvial flooding, terrestrial run-off transporting terrigenous material (e.g., humus substances, sediment), and freshwater discharge lowering the salinity and increasing nutrient inputs into the sea. Underwater light limitation due to freshwater discharge-related sediment and nutrient input will lead to a shallower growth maximum with a concurrent reduction in biodiversity for kelp, maërl, and seagrasses. Lower salinity and warming are also likely to reduce *Zostera marina* growth, density, and subsequently, their productivity and habitat complexity (Holmer and Bondgaard, 2001; Ehlers et al., 2008; Salo and Pedersen, 2014), the latter being essential for associated species. Given the predicted salinity decrease and warming of the Baltic Sea, these results supported the idea that isolates of wasting disease pathogen *Labyrinthula zosterae* do not represent an immediate risk for *Z. marina* beds in the Baltic Sea.

Finally, sea level rise would mostly affect salt marshes, although with some variability depending on species and regions. Indeed, in some cases, salt marshes are currently able to keep up with sea level rise considering high enough accretion rates (Ladd et al., 2019), but in other cases, the extent area of the ecosystem has already started declining or is projected to decline in the future (Duarte et al., 2021; Richards et al., 2008; Carrasco et al., 2021). For instance, the native *Spartina* spp. shows a higher tolerance to inundation related to sea level rise. However, a shift from this perennial plant to the annual succulent *Salicornia veneta* has already been observed under the combined effect of heat waves and drought, increasing the long-term vulnerability of the ecosystem in the face of sea level rise (Strain et al., 2017). Furthermore, there is also quite a variability depending on the model used to predict future sea level rise scenarios. For example, physical models such as general atmosphere-ocean circulation models reported increments of 0.28–0.98 m in 2100, with respect to the levels in 1986–2005 (Church et al., 2013), while semi-empirical models report predictions by 2100 of 0.5–1.4 m, with respect to 1990 levels (Vermeer and Rahmstorf, 2009) or 0.57–1.1 m by 2100 considering the levels in 1980–2000 (Jevrejeva et al., 2012). More recent studies that considered ice-sheet contributions have estimated that the global mean sea level could exceed 2 m by 2100 with respect to the levels in 2000 (DeConto and Pollard, 2016). Predicting how salt marshes and other MCEs in the North-East Atlantic are going to be affected by sea level rise, therefore, remains a significant challenge.

4.3.1. Management recommendations in North-East Atlantic

4.3.1.1. Improve water quality by reducing nutrient and sediment load.
Nutrient enrichment from run-off can cause the opportunistic algae to overgrow the kelps, maërl and seagrasses, limiting light and CO_2 availability for healthy growth. Increased ammonium loading due to freshwater discharge will amplify the adverse effect of low salinity on growth-related variables and survival in *Z. marina*, putting estuarine seagrass beds particularly at risk (Villazán et al., 2015). Overall, MCEs in North-East Atlantic are all vulnerable to terrestrial run-off, sedimentation, and nutrient loading from agriculture, aquaculture, and coastal development. All those local stressors that strongly affect the water quality should be the primary focus of coastal management, knowing that some MCEs contribute to increased water quality, like seagrass beds, salt marshes or kelp forests. Still, reducing nutrient releases through better treatment of sewage and lowering fertiliser use could counteract the excessive growth of epiphytes over vegetated coastal habitats.

4.3.1.2. Allow recovery by reducing coastal and marine resources exploitation.
Overfishing may lead to the same result as nutrient enrichment, creating a cascade effect. Removing large predatory fishes will increase the number of smaller fishes that eat the grazers (e.g., snails and small crustaceans). With fewer grazers, the epiphytes can flourish. In combination with other local factors, the replacement of kelp forests by turf communities (Filbee-Dexter and Wernberg, 2018; Nepper-Davidsen et al., 2019; Moy and Christie, 2012) would have a severe impact on the ability of kelp to re-establish because of a thick sediment layer on the bottom trapped by turf communities, preventing kelp spores from finding a hard bottom substrate where they can germinate. Pessarrodona et al. (2021) showed that the shift from kelp communities to ground-covering turf assemblages resulted in global miniaturisation and homogenisation of underwater habitat structures. Therefore, sustainable management of coastal fisheries (artisanal and recreational) is a priority too. Local removal actions of sea urchins could help kelp forest ecosystems by releasing the grazing pressure and avoiding shifting into large, denuded areas. In the last decades, harvesting wild kelp populations at sea has increased in northern Europe, where kelp is used as human food, a source of alginate for many applications, fertiliser for agriculture, and biofuel production (Peteiro et al., 2016). The implementation of long-term conservation measures is necessary for sustainable exploitation and the protection of the resource.

4.3.1.3. Promote a better management of coastal urbanisation.
Given sea level rise predictions, salt marshes' integrity could be at stake. Ensuring salt marshes have enough space to shift inland as sea level rises and restoring sediment inputs would maintain their presence and the services they provide to coastal communities, particularly controlling coastal erosion and protecting our coastline against flooding and storm surge events. Policy towards coastal management should continue moving away from land claims for economic growth in favour of salt marsh conservation to maintain the seascape's integrity and sustain ecosystem services (Foster et al., 2013; Ladd et al., 2021).

4.4. Knowledge gaps and future recommendations for assessing safe operating space and thresholds

Limitations that inevitably come with an extensive literature review also mean that many valuable articles, or grey literature, could have

been missed in English or other languages. Additionally, as this review focused on the effects of climate change with or without local stressors and conditioned by a list of keywords relative to thresholds or safe operating spaces, many valuable studies were omitted, including the ones looking solely at the impact of local stressors. Despite those limitations, the effects of climate change drivers are relatively well-defined in the scientific literature, although their interaction and the frequency of consequent events (e.g., extreme weather, heat waves) remain poorly studied. However, important knowledge gaps remain, mostly about their interaction with local stressors, many of which, such as recreational activities (anchoring, recreational fishing) in the Mediterranean Sea, holopelagic Sargassum rafts in the Caribbean (Banaszak, 2021), aquaculture in North-East Atlantic (Haugland et al., 2021) along with global pressures such as pollution, marine litter, over-sedimentation, bottom trawling, and hydrologic disturbances that are known to impact MCEs and therefore, affect their resilience to climate change drivers (Boudouresque et al., 2009; Orth et al., 2006; Fragkopoulou et al., 2021; Lincoln et al., 2022).

Information on thresholds and safe operating space were retrieved from the literature for most ecosystems for at least one CC-related pressure. However, the current state of knowledge also highlights the difficulty of precisely determining thresholds and safe operating spaces, but see Papaki et al. (2020), who used current seagrass distribution in the Mediterranean with environmental conditions to identify safe operating spaces. Experiment size, costs, and project time constraints often limit experimental settings to test two or three temperature targets based on IPCC-predicted future scenarios. Therefore, it is difficult to establish when a threshold for an environmental factor is exactly crossed (de Juan et al., 2018). Furthermore, the complex interactions with other climate change drivers and local stressors make thresholds not fixed values, and we were not able to assess the effect of local stressors on those CC thresholds or safe operating space from this literature review.

Another limitation when investigating threshold values for CC drivers and local stressors is that these have only been experimentally tested for a limited number of coral or salt marsh species, for instance, and responses can vary significantly between species. For example, corals' control of pH and calcification response are species-specific and have only been tested for very few species. Knowing the thresholds and optimal values for a few species limits our capacity to translate physiological responses to population and community as coral reefs are diverse ecosystems. Some species interaction studies conclude that the response of the maërl bed community to climate change will be strongly conditioned by changes in species interactions (Legrand et al., 2017).

Local biophysical factors may affect acclimatisation potential further hampering the establishment of species-specific threshold values for MCEs. For instance, in the temperate North-East Atlantic, the seagrass *Z. marina* is distributed along an extensive thermal range from low to high latitudes. Their populations respond differently to heat stress, with the southern population recovering faster from heat stress than the northern population (Winters et al., 2011; Jueterbock et al., 2016), which also has been shown for *P. oceanica* populations studied along a latitudinal gradient in the Mediterranean Sea's (Beca-Carretero et al., 2018).

In addition, benefits arising from the connectivity between MCEs could increase the adaptive capacity of MCEs to cumulative pressures. For example, mangroves can reduce bleaching susceptibility by providing light refugia to corals (Stewart et al., 2021), while coral reefs protect mangrove communities (Wegner and Ellis, 2017) and seagrass beds against waves and storms. These mutual synergies increase the resilience and services of individual MCEs to different stressors. They should, thus, be further explored, particularly in relation to the combined effects of climate change and local stressors.

5. Conclusion

As illustrated in this review, environmental conditions in the different ecoregions are changing with time, and climate change and local stressors can considerably affect the physiology of foundation species, populations, and communities. The potential impacts that could arise from co-occurring climate change and local stressors have started to be defined and quantified, but many have not been tested yet, or the effects remain unclear. Given species-specific nonlinear responses and thresholds, we can still anticipate future climate impacts from the reviewed ecological studies. Some authors have even been able to simulate IPCC scenarios on MCEs, using the upper tolerance limit for several species to predict future distribution if the temperature is increasing (Assis et al., 2016; Assis et al., 2018; Fernández-Martínez et al., 2019). This review highlights the need for a more comprehensive, multi-species, multi-ecosystems, and multi-stressors approach to predict better changes at the ecosystem and seascape levels of MCEs. Research needs broad-spanned long-term monitoring of the ecological condition and extent of MCEs, using field-based surveys coupled, if relevant, with remote sensing applications. These prolonged monitoring programs and observational networks are necessary for detecting and attributing ecological changes in response to climate change and other human pressures. Furthermore, research should continue with laboratory and field process studies, manipulative experiments, and modelling from small-scale process simulations to large-scale coupled biophysical models. Developing ambitious management techniques such as nature-based solutions to maintain, enhance or recover the ecological condition of MCEs is thus an urgent need to build more resilient ecosystems to face climate change threats. While it is difficult to predict future changes, improving ecological forecasting capabilities to support climate adaptation strategies and policy decisions is key for effectively implementing nature-based solutions.

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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

Data will be made available on request.

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