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REVIEW

Impacts of marine heatwaves in coastal ecosystems depend on local environmental conditions

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Abstract

Marine heatwaves (MHWs), increasing in duration and intensity because of climate change, are now a major threat to marine life and can have lasting effects on the structure and function of ecosystems. However, the responses of marine taxa and ecosystems to MHWs can be highly variable, making predicting and interpreting biological outcomes a challenge. Here, we review how biological responses to MHWs, from individuals to ecosystems, are mediated by fine-scale spatial variability in the coastal marine environment (hereafter, local gradients). Viewing observed responses through a lens of ecological theory, we present a simple framework of three 'resilience processes' (RPs) by which local gradients can influence the responses of marine taxa to MHWs. Local gradients (1) influence the amount of stress directly experienced by individuals, (2) facilitate local adaptation and acclimatization of individuals and populations, and (3) shape community composition which then influences responses to MHWs. We then synthesize known examples of fine-scale gradients that have affected responses of benthic foundation species to MHWs, including kelp forests, coral reefs, and seagrass meadows and link these varying responses to the RPs. We present a series of case studies from various marine ecosystems to illustrate the differential impacts of MHWs mediated by gradients in both temperature and other co-occurring drivers. In many cases, these gradients had large effect sizes with several examples of local gradients causing a 10-fold difference in impacts or more (e.g., survival, coverage). This review highlights the need for high-resolution environmental data to accurately predict and manage the consequences of MHWs in the context of ongoing climate change. While current tools may capture some of these gradients already, we advocate for enhanced monitoring and finer scale integration of local environmental heterogeneity into climate models. This will be essential for developing effective conservation strategies and mitigating future marine biodiversity loss.

KEYWORDS
coral reefs, environmental heterogeneity, extreme events, foundation species, global warming, kelp forests, microclimate, seagrass meadows

1 | INTRODUCTION

Understanding and predicting the ways that climate change is impacting our biosphere remains a considerable challenge. As the planet continues to warm, climate change is expected to drive sustained and heightened impacts on marine ecosystems (Hoegh-Guldberg et al., 2019; Pörtner et al., 2019; Wernberg et al., 2024), threatening the persistence of individual taxa as well as the ecological functioning of ecosystems (Pörtner et al., 2019). A key manifestation of climate change in the ocean is the amplification of marine heatwaves (MHWs) which are becoming more frequent, longer, and more intense as greenhouse gas emissions continue (Frölicher et al., 2018; Oliver et al., 2019). MHWs are periods of unusually warm water and they have the potential to drastically alter ecosystems if they are intense enough to surpass key temperature thresholds for sustained periods (Hughes et al., 2018; Smale et al., 2019; Wernberg et al., 2024). As MHWs become longer and more extreme, they are emerging as the dominant threat to some of the most diverse and productive marine habitats, including coral reefs, seagrass meadows, and kelp forests (Hughes et al., 2018; Pörtner et al., 2019; Smale et al., 2019; Strydom et al., 2020; Wernberg et al., 2024). Thus, to increase our capacity to mitigate these impacts, there is significant onus on marine ecologists to understand and predict how MHWs have, and will continue to, impact marine ecosystems around the globe. Despite this imperative, there remains substantial unexplained variation in the responses of marine taxa to these events (Bates et al., 2018; Smith et al., 2023).

The underlying environmental context over which an MHW occurs strongly influences its impacts, contributing to variability in biological responses. For example, species and populations living in environments that already approach or exceed their thermal safety margins are the most likely to be negatively impacted by MHWs (Filbee-Dexter et al., 2020; Smith et al., 2023), and thus, warm range-edge populations are often sensitive to MHWs (e.g., Bennett et al., 2015; Cavanaugh et al., 2019; Wernberg et al., 2016, 2024). In contrast, while MHWs are generally associated with negative impacts on existing coastal habitats [e.g., mass coral bleaching (Hughes et al., 2018; Smith et al., 2023; Wernberg et al., 2024)], they may positively affect species in environments cooler than their thermal optima (Ishida et al., 2023; Smale et al., 2017). Thus, it has long been appreciated that MHWs vary in their impacts across coarse-scale geographic gradients such as latitude (e.g., Sully et al., 2019; Wernberg et al., 2016). But while predictive models and ecological theory may offer expectations for how species will respond toward range edges (Bennett et al., 2015; Day et al., 2018; Pinsky et al., 2020), the dynamic nature and complexity of coastal systems can drive wide variability in environmental conditions across even short distances and small areas (e.g., Helmuth et al., 2014; Starko et al., 2019, 2024). Thus, impacts brought on by MHWs are likely to be highly variable on small scales within the geographic ranges of taxa.

Ecologically relevant variation in environmental factors occurring at the local scale (meters to kilometers as defined by Poiani et al., 2000) is ubiquitous in nature and has the potential to explain substantial variability in biological responses to climate change. Local-scale environmental variation strongly structures marine ecosystems, for example, by determining physiological rates (Filbee-Dexter et al., 2022; Tewksbury et al., 2008), altering interactions (Tylianakis & Morris, 2017), and driving the composition of ecological communities (e.g., through "environmental filtering": Diamond, 1975; Kraft et al., 2015). It, therefore, follows that this variation in the environment is likely to strongly underlie biological responses to environmental change, including responses to extreme MHWs. However, the fine-scale nature of this variation can make it challenging to characterize. For example, while satellite-based sensors may record surface temperature at a sufficient resolution to capture some of this variability, environmental variation at the finest of scales generally requires on-the-ground observation to capture relevant variation (Potter et al., 2013).

Growing evidence suggests that latitude does not always predict temperature at small scales due to complex shoreline features and oceanographic processes (e.g., Starko et al., 2024; Verdura et al., 2021; Woesik et al., 2012), which cause local hotspots or cool spots that can influence the local-scale temperatures experienced during regional scale MHWs. Moreover, this fine-scale temperature variation can often be missed by satellite thermal bands (e.g., MODIS Aqua), oceanographic models (e.g., Copernicus), global climatology layers (e.g., BioOracle), or climate models (e.g., CMIP6 model suite), which rely on coarse cell sizes, sometimes larger than the gradients themselves. For example, Copernicus and BioOracle have a resolution of 5 arcmin (~9 km) while CMIP6 ocean models have a resolution of 0.25° (~28 km). Consequently, studies and trackers (e.g., https://www.marineheatwaves.org/tracker.html) using these tools to explore the impacts of MHWs or of warming waters more generally may miss the mediating impacts of local-scale temperature variation that occur at the meters-to-kilometers scale. Local variation in abiotic factors other than temperature (e.g., nutrients, water motion, light availability; hereafter co-occurring factors) are also known to interact with temperature impacts, which can make species and ecosystems more sensitive or resilient to the impacts of warm conditions (Donovan et al., 2020, 2021; Fifer et al., 2021; Starko et al., 2019; Wernberg et al., 2024). This environmental variation emerges through a broad range of widespread natural and anthropogenic processes (e.g., freshwater run-off, tidal or wave processes, light attenuation with depth) and are ubiquitous in coastal waters. Moreover, these co-occurring factors are generally either not detectable using remote sensing tools or modeling approaches or, like temperature, can only be characterized at spatial scales larger than many of the gradients themselves. For example, the new Plankton, Aerosol Cloud, ocean Ecosystem (PACE) mission operated by the National Aeronautics and Space Administration (NASA) is capturing data on some relevant variables at 1 km resolution (Remer et al., 2019) which may be sufficient in some systems but may be too coarse for others.

Together, local variation in both temperature and other variables mediates the impacts of MHWs, causing a range of effects across any given coastline (e.g., Baum et al., 2023; Donovan et al., 2021; Fifer et al., 2021; Starko et al., 2019; Tait et al., 2021; Whalen et al., 2023). Thus, although complete species extinctions and drastic ecosystem reconfigurations have been reported in response to MHWs at regional scales (e.g., Wernberg et al., 2016), MHWs more often drive variable and patchy declines in the abundance or distribution of species, leading to heterogeneous impacts at fine scales (e.g., Donovan et al., 2021; Giraldo-Ospina et al., 2020; Starko et al., 2022; Whalen et al., 2023). Importantly, however, it is at these fine spatial scales that regulators and stakeholders attempt to understand and manage their systems in the face of ongoing global change (Helmuth et al., 2014), creating a disparity between the regional scales at which MHWs are measured (and responses to MHWs are most often studied and understood), and the local scales at which systems are experienced by organisms and overseen by managers.

Here, we review evidence showing that local environmental variation influences the responses of marine species and ecosystems to MHWs. Our aim is to synthesize observational studies that have characterized the mediating impacts of local environmental variation during MHWs and to contextualize these findings in ecological theory using a simple framework. We refer to local environmental variation as "local gradients." While we acknowledge that narrower definitions of the term "gradient" require the factor change unidirectionally, we mean it here in the broader sense of variation in an abiotic factor across space, regardless of the underlying structure of this variation. We begin with a brief overview of the physical processes that lead to local gradients and how they interact with MHWs. Next, we outline three key processes (hereafter Resilience Processes [RPs]; Figure 1) that link local variation to MHW responses and are each based on different facets of ecological theory:

> RP1. Local gradients influence the environmental conditions directly experienced by individuals, therefore impacting MHW exposure as well as performance and fitness outcomes (based on ecophysiological theory).
>
> RP2. Local gradients facilitate local adaptation and acclimatization that alter key temperature thresholds of individuals and populations (based on microevolutionary and ecophysiological theory).
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> RP3. Local gradients alter the species composition of communities, leading to different community-wide responses (based on community assembly theory).

We then identify several case studies in coastal marine ecosystems where local gradients have mediated the impacts of MHWs

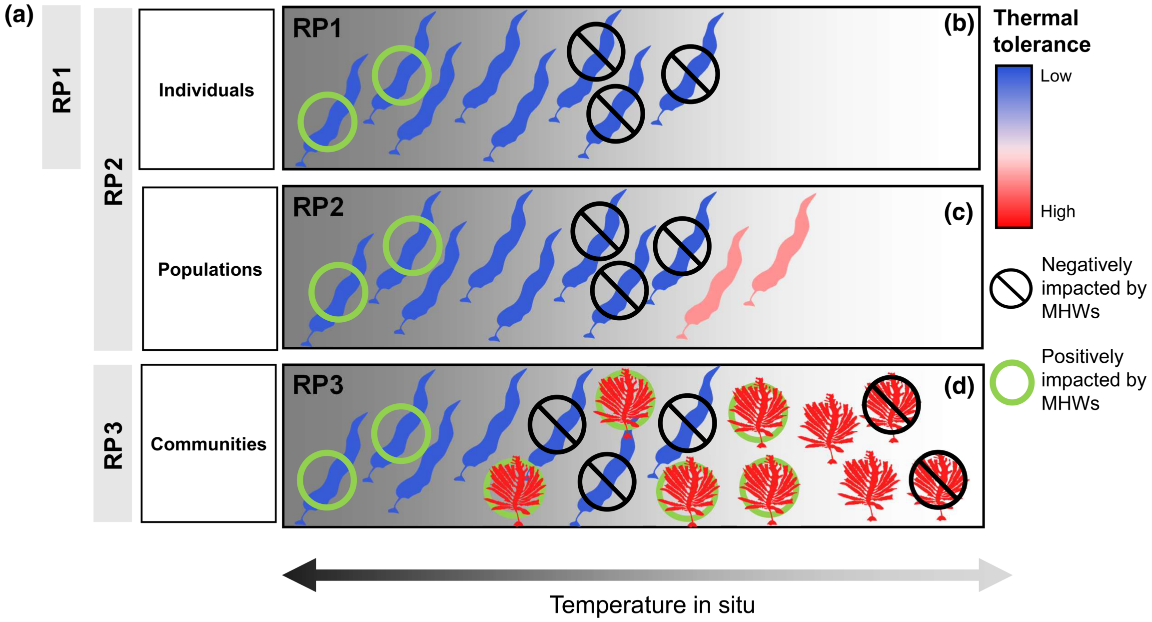

FIGURE 1 The resilience processes (RPs) that link local environmental gradients to the impacts of marine heatwaves (MHWs). (a) Levels of biological organization acted upon by each of the three RPs. (b–d) Examples of how RPs impact MHW responses across environmental gradients using a temperature gradient as an example. The *x*-axis shows a hypothetical local ocean temperature gradient. (b) RP1 results when a local gradient causes some individuals to be under more thermal stress than others, resulting in differential mortality across plots or sites. Individuals growing in areas that are in areas cooler than their thermal optimum may benefit from the MHW while those already growing above it may be most impacted, including likely mortality. (c) RP2 results when local adaptation or acclimatization cause individuals of the same species to have different thermal tolerances (warm-tolerant individuals shown in pink). This difference leads to outcomes that are challenging to predict but may lead to unexpected survival in the most thermally exposed populations. (d) RP3 results when an environmental gradient alters community composition due to differences in the physiological characteristics of species, and then constituent species differ in their responses to the MHW. In this case, some species may benefit while others may be negatively impacted.

and link each of these case studies to the relevant RPs. We focus our synthesis on marine habitat-forming (i.e., foundation) species because they play central roles in the structuring of ecosystems but are unable to move to avoid local conditions (Wernberg et al., 2024). Thus, unlike taxa that can move to cooler environments (e.g., deeper waters) during MHWs (Magel et al., 2020; Spence & Tingley, 2020), these species must endure the conditions directly imposed by MHWs. Moreover, the coastal environment which they inhabit offers a highly complex and heterogenous landscape of environmental variation (Bates et al., 2018; Helmuth et al., 2014). Bathymetric and topographic features such as shallow reef habitats, bays, fjords, and rivers, coupled with hydrodynamic and atmospheric processes, have the potential to drive substantial environmental variability (Akbari et al., 2017; Starko et al., 2024) that likely mediates the impacts of MHWs on these ecosystems.

While the formal definition of an MHW is a period of greater than 5 days where temperatures exceed the 90th percentile of historical baseline temperatures (Hobday et al., 2016), the exact method of calculating this (e.g., choice of baseline years) is debated (Rosselló et al., 2023; Sen Gupta, 2023). Moreover, many studies do not report MHWs in the context of this formal definition. For example, coral reef papers tend to calculate degree heating weeks instead of reporting MHW intensity and duration based on the Hobday et al. (2016) definition. In the present review, we chose to treat the definition of MHW more broadly and consider studies reporting any rapid increases in water temperatures extreme enough to elicit biological responses.

2 | LOCAL GRADIENTS AND HOW THEY MEDIATE MHW IMPACTS

2.1 | Drivers of local gradients and interactions with MHWs

Environmental variability exists across virtually all spatial scales in nature. On the local scale of meters to kilometers, gradients in key environmental variables generally arise through interactions of atmospheric and hydrodynamic processes with topographic and bathymetric features. Both thermal exchange between the ocean and atmosphere as well as interactions with local currents or hydrodynamic features can drive the emergence of local hotspots or cool spots. Interactions between tides, wind, and waves (surface and internal) and the bathymetry of a reef can, for example, impact the residence time of water in specific reef areas (e.g., Grimaldi et al., 2023). This impacts the advection of heat, which can generate distinct thermal environments separated by 100s of meters or less (Grimaldi et al., 2023; Morikawa & Palumbi, 2019; Palumbi et al., 2014). Similarly, bays and fjords that have high residence times can heat up disproportionately during warmer times of year (e.g., Hetzel et al., 2018; Inall & Gillibrand, 2010; Starko et al., 2022, 2024). Local and regional-scale currents, such as tidal currents (Berry et al., 2021) and eddies (McGillicuddy, 2016), can also lead to extreme temperature variability and can both mitigate (Li et al., 2023) and enhance (Chen et al., 2022) the local intensity of MHWs. Temperature also often varies strongly across depths (Akbari et al., 2017). For example, in some systems, stratification can drive temperature differences of several degrees over only a few meters as one moves from the surface to below the thermocline (Boguslavskii et al., 2004). Mixing due to wind, tides, and waves, as well as interactions between ocean currents and bottom topography (Melet et al., 2022), can disrupt stratification and lead to a well-mixed water column, potentially preventing the formation of warm surface waters above the thermocline.

These local temperature gradients are ubiquitous in marine systems and can interact with MHWs to produce a range of different realized outcomes during the event (Figure 2). For example, sites could differ in average temperature but experience MHWs of similar magnitudes (Figure 2a), resulting in the warmer sites reaching higher temperatures (e.g., Starko et al., 2022). Alternatively, temperature at some sites could be partially or completely decoupled from regional scale oceanography due to local-scale processes (Figure 2d) such as stratification across depths (e.g., Estaque et al., 2023). Although we commonly define and study MHWs as regional rather than local scale phenomena, variation in local conditions during MHWs can vary substantially across short distances with the potential to mediate biological outcomes across the seascape (Morikawa & Palumbi, 2019; Starko et al., 2022). In the most extreme case, decoupling of local and regional temperatures during a regionally detected MHW could cause refugial habitats to not experience an MHW at all on a local scale (e.g., Hemming et al., 2024).

Gradients in co-occurring factors are also ubiquitous in nearshore ecosystems. For example, the presence of river or creek mouths and other freshwater sources can impact the salinity of coastlines or the amount of suspended particulate matter (e.g., Druehl, 1978; Milliman & Syvitski, 1992), while evaporation can cause local increases in salinity (e.g., Riegl & Purkis, 2012; Wolanski, 1986). Moreover, nutrients can covary negatively with temperature (Kamykowski & Zentara, 1986), but be higher in the presence of human settlements (e.g., McDevitt-Irwin et al., 2019; Ziegler et al., 2019) and can be altered by regional or local currents (e.g., DeCarlo et al., 2020) or by local oceanography and topography (e.g., Druehl et al., 1988; Du et al., 2021). In addition to temperature, depth stratification can also lead to reduced oxygen concentrations near the bottom, since well-oxygenated surface waters are not mixed into the water column (e.g., O'Boyle & Nolan, 2010), or reduced nutrients at the surface due to microbial activity in warm conditions (Kamykowski & Zentara, 1986). Water characteristics (e.g., chemistry) can also directly impact the thermal tolerance of a wide range of taxa (e.g., Druehl, 1978; Gegner et al., 2017). Therefore, given the ubiquity of these gradients in nature, they are likely to be key mediators of biological impacts of MHWs.

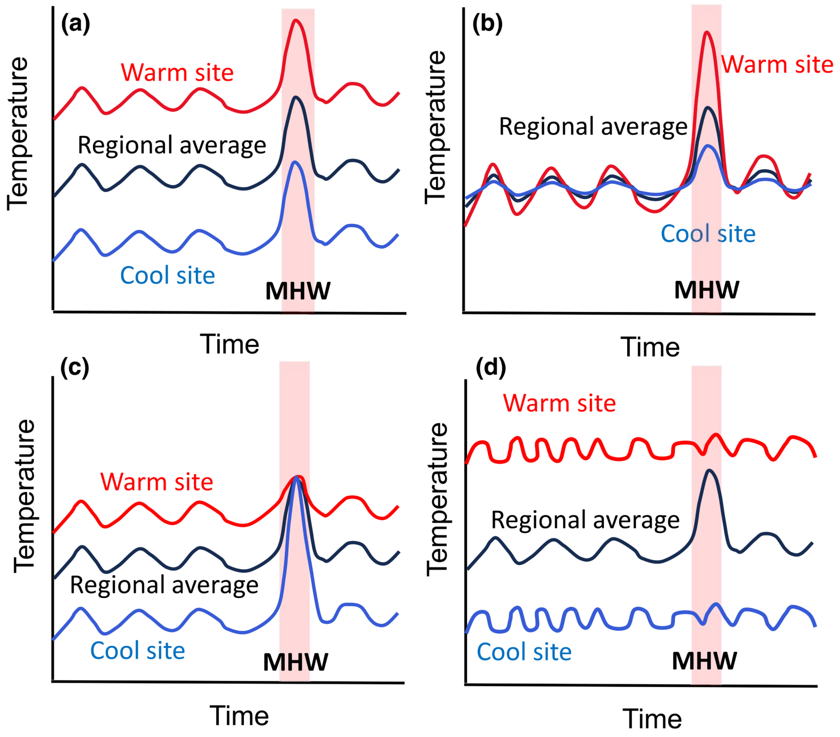

FIGURE 2 Possible interactions between marine heatwaves (MHWs) and local temperature gradients. Shown are hypothetical examples of how (a) warm and cool sites experience similar fluctuations in temperature (including during the MHW) but differ in average temperature (all sites experienced the MHW). (b) Sites that are locally warm during the MHW are more variable than the regional average and cool sites are less variable than the regional average (all sites experienced the MHW). (c) Sites typically vary in average temperature but during the MHW, temperatures are similar across all sites (cool site experiences strong MHW, warm site experiences mild MHW). (d) Some sites are completely decoupled from the regional average because temperatures are driven by processes other than regional oceanography (e.g., atmospheric warming or cooling). In this case, neither site experiences an MHW despite the regional event.

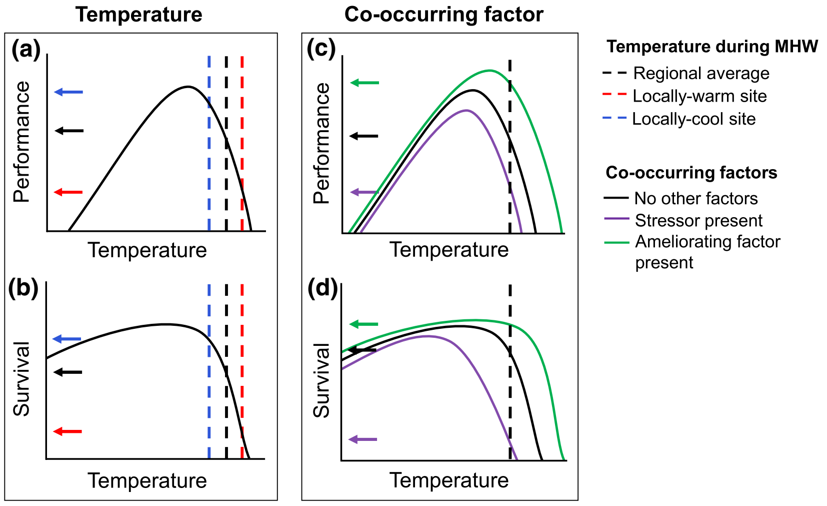

FIGURE 3 Conceptual figure depicting RP1, showing examples of how local environmental gradients influence the impacts of a marine heatwave (MHW) on individuals (top row; a, c) and populations (bottom row; b, d). Dotted lines indicate the temperature range of a hypothetical MHW and arrows (colored to match the different microhabitat scenarios) indicate the value on the *y*-axis that corresponds to each microhabitat scenario, assuming a constant thermal performance curve or mortality curve across different microhabitats (i.e., no local adaptation or plasticity occurring).

2.2 | RP1: Local gradients influence the environmental conditions directly experienced by individuals, therefore impacting performance and fitness outcomes

As MHWs unfold on broad scales, they are superimposed on pre-existing local gradients thereby influencing the actual conditions that organisms experience in nature (Figure 2). Modern physiological and metabolic theory (reviewed by Schulte, 2015) predicts that ecological and physiological outcomes in ectothermic organisms depend on the interaction between a species' thermal performance characteristics (quantified using thermal performance curves [TPCs]) and environmental temperature. For this reason, the response of a species to MHW conditions depends on where those environmental conditions during the event fall along their TPC. By influencing the specific temperatures reached during MHWs, local gradients in temperature can directly influence the impact of MHWs, including whether or not key thresholds (e.g., lethal temperatures) are crossed (Schulte, 2015). For example, individuals living in locally warm environments will experience greater absolute temperatures than those at cooler sites if a MHW occurs that universally increases temperatures by a certain amount (e.g., Figure 2a) and this can cause some areas to cross lethal environmental thresholds while others remain as refugia (Figure 3a) (Grimaldi et al., 2023; e.g., Starko et al., 2022; Verdura et al., 2021). In the most extreme circumstances, there may be situations where decoupling between local and regional conditions (due to winds, currents, depth, and other factors) causes an ecosystem to appear locally resilient to an MHW when in fact an MHW has never occurred at the local scale (Figure 2d). These habitats may serve as refugia during broader MHWs and represent a particularly extreme case of RP1. Importantly, the exact shape of TPCs and the temperatures at which lethal thresholds are crossed can depend on the duration of the MHW. Specifically, because acute thermal tolerance is generally greater than chronic thermal tolerance (e.g., Evensen et al., 2021; Johnstone & Rahel, 2003; Rezende et al., 2014), longer events require lower temperatures to cause mortality or other effects (Smith et al., 2023, 2024; Wernberg et al., 2024).

Because of the nonlinear nature of TPCs, ignoring local gradients can lead to biased predictions when assessing the impacts of an MHW across a variable landscape (Schulte et al., 2011). Jensen's inequality states that the average of a nonlinear function of a variable is not equal to the function of the average of that variable (see Denny, 2017; Ruel & Ayres, 1999). In the context of TPCs, this means that using regional average temperatures to predict local-scale biological responses during an MHWs may underestimate negative impacts, particularly when conditions are near or above optimal temperature, where the relationship between temperature and performance is often strongly nonlinear (Schulte, 2015; Schulte et al., 2011). In these cases, locally warm sites may experience substantial negative impacts that would be missed entirely by comparing regional average temperatures to species- or population-level TPCs.

Gradients in other environmental variables (e.g., nutrients, pollution, water motion, light) can also interact with temperature to mediate the impacts of extreme warming conditions (Bates et al., 2019; Claar et al., 2020; Maucieri et al., 2023) (Figure 3b). These gradients do so by altering the underlying shape of TPCs (Fernández et al., 2020; Verheyen & Stoks, 2023). For example, while a particular temperature may be benign in environments with certain seawater characteristics, they may become stressful under others [e.g., low salinity in kelp (Druehl, 1978)]. In the context of MHWs, environmental gradients that exacerbate climatic impacts are often studied under the theme of multiple stressors where global (i.e., climatic) and local pressures interact to drive biological responses (Bates et al., 2019; Darling et al., 2010; Orr et al., 2020). Substantial research has focused on multiple stressors in the context of MHWs and anthropogenic drivers (e.g., fishing pressure, pollution: Bates et al., 2019; Baum et al., 2023; Claar et al., 2020; Darling et al., 2010; Maucieri et al., 2023). However, natural gradients of environmental factors (e.g., light, nutrients) can also influence species' responses to warming waters (e.g., Li et al., 2020; Tagliafico et al., 2022; Tait et al., 2021). Moreover, particular environmental conditions ameliorate, rather than exacerbate, the impacts of MHWs (e.g., Fifer et al., 2021). For example, the availability of nutrients can alter the thermal performance of both habitat-forming seaweeds (positively: Fernández et al., 2020; Gerard, 1997) and reef-building corals (negatively: DeCarlo et al., 2020; Donovan et al., 2021; Vega Thurber et al., 2014) but in opposite directions.

2.3 | RP2: Local gradients facilitate local adaptation and acclimatization that alters key temperature thresholds

Local environmental gradients can influence the impacts of MHWs on individuals and populations by facilitating local adaptation that can make populations more sensitive or resilient to climate warming (Palumbi et al., 2014; Figure 2). Local adaptation arises when variation in fitness has a genetic basis and can be selected for by local conditions over generations (De Meester et al., 2011; Ellegren & Sheldon, 2008). Warmer localities can drive selection for thermally tolerant genotypes, potentially facilitating adaptations that benefit individuals during MHW events (McKay et al., 2001; Yampolsky et al., 2014). Individuals growing in environments that regularly experience drastic temperature variability and/or warmer-than-average temperatures (e.g., rock pools, lagoons) may already be adapted to conditions typical of MHWs and fare better during these events (Morikawa & Palumbi, 2019; Palumbi et al., 2014; Thomas et al., 2022). The extent to which local adaptation occurs depends in large part on the amount of connectivity between populations (Savolainen et al., 2007). Within a species, limited gene flow may facilitate rapid adaptation; however, some gene flow may help to ensure sufficient genetic variability is available to facilitate adaptive changes in relevant traits (Savolainen et al., 2007; Tigano & Friesen, 2016).

Local environmental gradients can also facilitate phenotypic plasticity, or variation in phenotypic responses that are not due to underlying genetic variation (West-Eberhard, 1989). Thermal acclimatization (i.e., physiological plasticity in thermal tolerance) occurs when an individual that has experienced warm (or cool) conditions in the past is more physiologically capable of withstanding those conditions again. This is well known to occur across a wide range of species and may underlie resilience in some systems (Palumbi et al., 2014; Somero, 2010). Furthermore, plasticity can sometimes be heritable and persist over longer timescales through processes such as epigenetics (Galloway & Etterson, 2007). Critically, local gradients may drive a combination of both adaptation and phenotypic plasticity concurrently, altering thermal tolerance phenotypes across sites (Figure 4). This may facilitate improved performance of individuals under conditions expected during MHWs. However, if locally warm sites heat up more than locally cool sites during these events, the outcome of this can be challenging to predict. Here, the outcome would depend on how the absolute temperatures reached at each site compare to the thermal performance characteristics of locally adapted or acclimatized individuals (Figure 4).

In American Samoa, corals growing in back-reef pools with high temperature variability (including frequent exposure to high temperatures) are more thermally tolerant than corals growing in pools with less temperature variability (Morikawa & Palumbi, 2019; Palumbi et al., 2014). Transplant experiments showed that this was the result of both plasticity and local adaptation in the face of warmer conditions (Palumbi et al., 2014). An experiment that both tracked colonies in situ and out-planted fragments of each colony in a common garden found reduced bleaching during a natural MHW in samples sourced from parts of the reef that experienced greater thermal variability (including greater temperatures: Morikawa & Palumbi, 2019). This clearly demonstrates the importance of local microclimate in driving patterns of thermal adaptation and acclimatization in corals and therefore their susceptibility to MHWs.

2.4 | RP3: Local gradients alter the species composition of communities, leading to different community-wide responses

Local environmental gradients can also influence higher level community- or ecosystem-level responses to MHWs by altering the species that are present in a particular place (Bates et al., 2019; Kraft et al., 2015), thereby influencing the degree to which communities and ecosystems are impacted by warm waters. Community assembly theory predicts that gradients of temperature or other stressors can filter out species based on key traits (Chase, 2003; Diamond, 1975). In this way, species that are sensitive to environmental change may be excluded from particular localities, increasing the resistance of resultant communities and ecosystems to warm waters during MHWs (Figure 5). Local gradients can also mediate species interactions, potentially altering the species that are removed through biotic filters (e.g., Randell et al., 2022). In this way, environmental gradients can act as an extinction filter, removing species that may be sensitive to climate change before they have experienced its impacts (Balmford, 1996). Under this mechanism, communities exposed to particular local conditions may be made

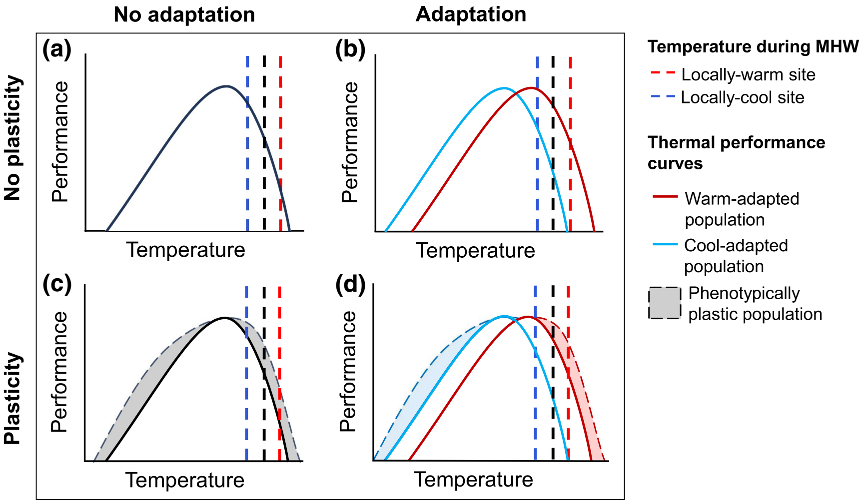

FIGURE 4 Conceptual figure depicting RP2, showing examples of how adaptation and phenotypic plasticity influence the thermal tolerance of individuals and populations, impacting their responses to MHWs. Shown are TPCs from populations with (a) no local adaptation or phenotypic plasticity to locally warm sites, (b) local adaptation but no phenotypic plasticity, (c) phenotypic plasticity but no local adaptation and (d) both local adaptation and phenotypic plasticity. While shaded regions in panel c should be present on both sides of each curve (e.g., the cool side of the warm-adapted population), some of the shading has been removed to reduce crowding. Vertical dotted lines indicate temperature extremes reached though hypothetical MHWs as in Figure 3. Overall performance during the MHW is equal to the intersections of the dotted lines and the TPCs. MHW, marine heatwave; TPC, thermal performance curve.

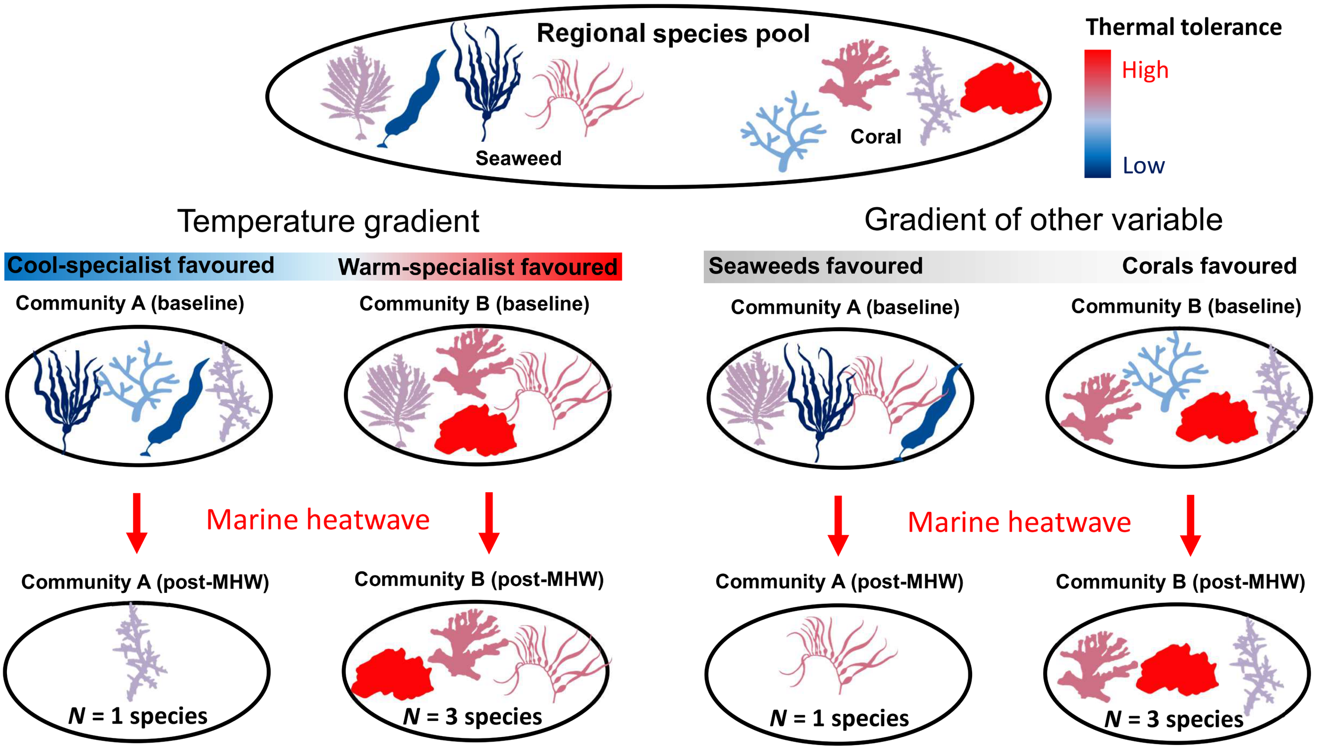

FIGURE 5 Simplified conceptual model for how local gradients filter species, thereby altering responses to warming. The top bubble indicates the regional species pool with four species of kelp and four species of coral that overlap in thermal tolerance. These species are then filtered into communities contingent on their thermal tolerance traits (left example) or taxonomy (coral vs. kelp; right example). Following a marine heatwave (MHW), communities are filtered further by their thermal tolerance, resulting in communities with differing community composition and species diversity.

up of species that are less sensitive to climate warming than they would be otherwise. This may cause apparent resilience in commonly reported community or ecosystem health metric such as diversity, coral bleaching, or coverage (Darling et al., 2010; Maucieri et al., 2023; Whalen et al., 2023).

RP3 is a key mechanism explaining the protection paradox in which communities protected from human disturbance are more sensitive to the impacts of climatic stressors. These impacted communities host species that are more tolerant of stress in general (reviewed by Bates et al., 2019), and therefore, they are less sensitive to MHWs. For example, in the absence of human disturbance (e.g., pollution, fishing), coral reefs tend to be dominated by corals from the "competitive" and "weedy" functional groups (sensu Darling et al., 2012), which are then highly sensitive to MHW-induced heat stress (Bates et al., 2019; Baum et al., 2023; Darling et al., 2013). Conversely, regularly disturbed coral reefs tend to be made of stress-tolerant coral species that are also resistant to heat stress (Baum et al., 2023; Darling et al., 2010). In this way, MHW impacts on regularly disturbed coral reefs may be less severe compared to coral reefs dominated by thermally sensitive taxa due to low levels of disturbance. Recent studies suggest that there is a level of human disturbance beyond which the protection paradox no longer applies and instead disturbed communities are disproportionately impacted by MHWs (Baum et al., 2023; Maucieri et al., 2023). This is likely because, at a certain point, stressors may become too intense for even the most resistant taxa.

2.5 | Interactions between RPs

Importantly, RPs are not mutually exclusive, and these processes may be occurring simultaneously at different levels of biological organization. Both RP1 and RP2 are based on interactions between environmental conditions and TPCs and are therefore likely to be interdependent. For example, a locally adapted population may require warmer absolute temperatures to cross-lethal thresholds (Palumbi et al., 2014). In host-associated microbial systems, community assembly (RP3) in the microbial community can drive acclimatization (RP2) in the host. Local gradients of both temperature and other environmental variables (e.g., nutrient pollution) can affect the microbial symbiont communities, directly influencing their thermal tolerance. In corals, for example, relative proportions of *Cladocopium* spp. and *Durisdinium* spp. explain variation in coral bleaching and mortality during MHWs in taxa that associate with both (Baker et al., 2004; Claar et al., 2020; Rose et al., 2021) and shifts between these two genera can be driven by fine-scale environmental variation (Baker, 2003). Consequently, thermal acclimatization (i.e., RP2) of corals often involves environmentally driven changes in the microbial community involving RP3.

3 | KEY GRADIENTS IN THE MARINE ENVIRONMENT AND THEIR KNOWN IMPACTS

We reviewed the literature for cases where local-scale environmental variation has mediated the responses of coastal foundation species to MHWs. We identified 25 real-world case studies where local gradients mediated the impacts of MHWs on marine species or communities. We then linked each of these to the underlying RPs (Table 1). We found examples of mediating effects from local gradients including temperature, water movement, water chemistry, and light, as well as compound factors that represent gradients of multiple parameters including human disturbance, distance from shore, and depth. We quantified the size of these mediating effects using a response ratio which we calculated by taking a ratio of the impacts of the MHW (e.g., proportional decline) on one end a local gradient versus the effect on the other end of the gradient. The strength of the mediating effect of local gradients in the case studies were highly variable, but in some cases, organisms varied by an order of magnitude or more in their responses, depending on the position of sites along local gradients (Figure 6).

3.1 | Local temperature variation

We identified case studies of local temperature gradients impacting responses to MHWs involving RP1 and RP2 (Table 1). However, RP1 appears to be the most common process driving variability in MHW responses along local temperature gradients. These case studies span a wide range of geographic localities and spatial scales from a few centimeters to tens of kilometers, and include kelp forests, seagrass meadows, and coral reefs. For example, survival of individual tagged kelps in Southern Norway during the 2018 MHW depended on site-specific maximum temperatures which varied over a few kilometers (Figure 6). Similarly, thermal heterogeneity across the coast of Southern British Columbia, Canada, strongly predicted kelp persistence through the prolonged 2014–2016 MHW, with losses in that region concentrated at locally warm hotspots (e.g., >20°C vs. 12–15°C) (Starko et al., 2019, 2022, 2024) (Figure 7). Local variation in temperature also explained the responses of seagrass habitats to the same MHW in coastal Oregon, United States, with considerably greater impacts in shallower habitats that warmed up significantly more during the event (Magel et al., 2022; Marin Jarrin et al., 2022). Local temperatures can also vary substantially within a coral reef, with examples of back reef pools experiencing more thermal variability due to tides, wind, and waves well documented in both American Samoa and NW Australia (Grimaldi et al., 2023; Palumbi et al., 2014). This is known to impact coral resilience to MHWs through both adaptation and acclimatization (RP2) (Morikawa & Palumbi, 2019; Palumbi et al., 2014; Thomas et al., 2022) including through community-wide shifts in host-associated microbial communities (RP3 for microbes, RP2 for host) (Palumbi et al., 2014).

Despite the clear importance of local temperature variability in mediating responses to MHWs, studies demonstrating RP2 and RP3 in marine systems remain limited. Except for host-associated microbial communities, we are unaware of any studies documenting RP3 in response to a local temperature gradient. One possible reason for this is that local temperature gradients are generally seasonally dependent. For this reason, all sites in a region (locally warm and cool sites) may experience cool winters, preventing warm-specialist species from establishing at locally warm sites over longer time periods (e.g., Lesk et al., 2017) and leading to cold-biased communities in locally warm areas. RP3 has been demonstrated with respect to depth, however, with temperature a key variable that changes across depths (Akbari et al., 2017). Nonetheless, understanding the extent to which local temperature gradients affect biological impacts through RP3 remains a critical knowledge gap. While work in American Samoa (Morikawa & Palumbi, 2019) provides an excellent example of local temperature-driven RP2 influencing biological impacts of MHWs and work in Western Australia highlights the potential for local adaptation of corals across local-scale temperature gradients (Thomas et al., 2022), the extent to which this occurs across other coral systems or other ecosystems more generally also remains poorly understood.

3.2 | Water movement (waves and currents)

There is growing evidence that water motion can impact biological responses to MHWs (e.g., Fifer et al., 2021; Starko et al., 2024), although the exact mechanism is not always clear. While waves and currents can cause mixing, potentially increasing nutrient concentrations and cooling surface waters through local upwelling (each of which can influence the MHW responses), water motion itself can mediate MHW impacts, even in the absence of these secondary drivers (Fifer et al., 2021). Water motion from waves and currents can reduce the thickness of boundary layers around organisms, increasing rates of exchange with the environment (Nakamura & van Woesik, 2001), potentially increasing their ability to withstand MHW conditions. However, water motion can also act as sources of disturbance, breaking or dislodging organisms, especially if their structural or material integrity is impacted by warming (Simonson et al., 2015). Thus, flow speeds and flow characteristics can play important roles in modulating the impacts of MHWs.

Among stony corals, current speed has been linked to bleaching resistance with reduced bleaching during MHWs among corals experiencing greater flow (Fifer et al., 2021; Raymundo et al., 2017). For example, during the 2014–2015 bleaching events on Guam, acroporid corals found near the well-flushed reef-crest experienced less bleaching than other parts of the reef (Raymundo et al., 2017). Transcriptomics revealed that genes associated with thermal tolerance are front loaded in colonies exposed to water motion, offering a potential mechanism for this phenomenon (Fifer et al., 2021) that is consistent with acclimatization (RP2). Coastal areas with

TABLE 1 Case studies ($n = 25$) that have demonstrated differential impacts of MHWs across local environmental gradients.

Study	Study ID	Gradient	Ecosystem	Location	Relevant resilience process	Geographic scale	Year of MHW	Outcome
Filbee-Dexter et al. (2020)	1	Temperature	Kelp forests	Southern Norway	RP1	A few to 10s of kilometers	2018	Increased mortality of tagged kelp at locally warm sites
Starko et al. (2022, 2024)	2, 4	Temperature	Kelp forests	BC, Canada	RP1	A few to 10s of kilometers	2014–2016	Increased kelp loss in locally warm waters; local refugia in high flow, cool environments
Verdura et al. (2021)	3	Temperature	Seaweed forests	Catalonia, Spain	RP1	10s of kilometers	2015	Decreased mortality of habitat-forming *Ericaria* in locally cool refugia
Marin Jarrin et al. (2022)	5	Temperature	Eelgrass	Oregon, USA	RP1	A few kilometers	2015–2016	Increased eelgrass damage in shallower, warmer estuaries
Morikawa and Palumbi (2019)	6	Temperature	Coral reefs	American Samoa	RP2	100s of meters	2015	Decreased bleaching in corals locally adapted to high temperature variability
Estaque et al. (2023)	7	Depth (temperature)	Octocorals	Northwest Mediterranean Sea	RP1	A few to 10s of meters	2022	Decreased coral necrosis on deeper reefs associated with colder waters
Gambi et al. (2010)	8	Depth	Gorgonian	Palinuro, Western Mediterranean	RP1	A few meters in depth (linear distance unknown)	2008–2009	Decreased coral mortality on deeper reefs
Giraldo-Ospina et al. (2020)	9	Depth	Kelp forests	Western Australia	RP1	100s of meters to a few kilometers	2011	Decreased kelp mortality on deeper reefs
Hoegh-Guldberg and Salvat (1995)	10	Depth	Coral reefs	Mo'orea, French Polynesia	RP2?, RP3	A few meters in depth (linear distance unknown)	1994	Greater bleaching of individual species (*Pocillopora*) at increased depth (RP2?). Decreased total bleaching at greater depth because of differences in species composition (RP3)
McField (1999)	11	Depth	Coral reefs	Belize	RP1	A few meters to a few kilometers	1995–1996	Bleaching differed substantially between depth (forereef vs. backreef) and this effect varied across species
Monroe et al. (2018)	12	Distance from shore; depth	Coral reefs	Central Saudi Arabia	Likely RP1, RP3	A few meters to 100s of kilometers	2016	Increased coral bleaching at inshore reefs which are less well flushed and at shallower depths within each site
Montefalcone et al. (2020)	13	Exposure (lagoon vs. outer reef); human disturbance	Coral reefs	Maldives	Likely RP1, RP3	A few to 10s of kilometers	2016	Reduced mortality on outer reefs and on atolls with less human disturbance
Whalen et al. (2023)	14	Vertical elevation	Rocky intertidal	BC, Canada	RP1, RP3	Centimeters to meters	2014–2016	Percentage cover of seaweeds decreased more during an MHW at higher intertidal elevations than at lower elevations

TABLE 1 (Continued)

Study	Study ID	Gradient	Ecosystem	Location	Relevant resilience process	Geographic scale	Year of MHW	Outcome
Zhao et al. (2023)	15	Depth	Coral reefs	Guangdong-Hong Kong-Macao Greater Bay Area	Likely RP1	A few meters in depth (linear distance unknown)	2022	Decreased coral bleaching on deeper reefs
Baum et al. (2023); Claar et al. (2020); Maucieri et al. (2023); Starko et al. (2023)	16–19	Human disturbance	Coral reefs	Kiritimati, Kiribati	RP1, RP2, RP3	A few to 10s of kilometers	2014–2015	Increased coral mortality in areas exposed to high human disturbance linked to multiple processes
Darling et al. (2010)	20	Human disturbance	Coral reefs	Kenya	RP3	A few to 150 km	1998	Increased mortality at reefs inside rather than outside protected areas due to differences in coral community composition
Berkelmans and Oliver (1999)	21	Salinity (distance from shore)	Coral reefs	Great Barrier Reef, Australia	RP1	A few to 100s of kilometers	1998	Higher levels of bleaching at inshore reefs linked to reduced salinity in these areas
Iluz et al. (2008)	22	Light	Coral reefs	Ile Alphonse, Seychelles	RP1	A few meters?	1997–1998	Lower mortality in the lagoon than on reef slopes because leaf litter reduced light in the lagoon
Raymundo et al. (2017)	23	Water motion	Coral reefs	Guam	RP1	100s of meters	2014, 2015 (2 events)	Decreased coral bleaching in areas exposed to tidal currents and flushing
Donovan et al. (2020)	24	Nitrogen	Coral reefs	Mo'orea, French Polynesia	RP1	A few to 10s of km	2016	Bleaching positively correlated with environmental nitrogen from human input
Furby et al. (2013)	25	Distance from shore	Coral reefs	Thuwal, Saudi Arabia	RP3	A few meters to a few kilometers	2010	Higher bleaching prevalence at inshore reefs, mostly linked to differences in species composition

Note: Resilience processes appended with a "?" indicate that the mechanism is assumed but not stated in the original study. Study ID refers to the ID numbers shown in Figure 6.

Abbreviation: MHW, marine heatwave.

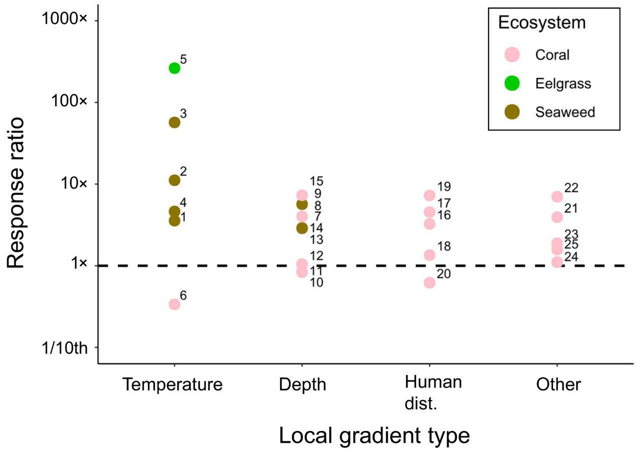

FIGURE 6 Relative impact of marine heatwaves on different ends of local gradients for 25 case studies discussed in this review. Values (response ratio) indicate how many times greater an impact was under one condition versus another. Temperature data indicate impacts at warm versus cool sites (positive = larger impact at cooler site), depth data are comparing shallow versus deep (positive = larger impact in the shallows), human disturbance indicates high versus low human disturbance (positive = larger impact in disturbed area), while the following are shown under other: Flow (positive = larger impact in high flow), light (positive = larger impact at site with more light), nutrients (positive = larger impact in high nutrients), and shore distance (positive = larger impact at sites closer to shore). Numeric labels on each data point correspond to study IDs in Table 1.

high waves or currents in Washington and British Columbia have remained more stable in the face of recent warming and MHWs than those found in inland waters that experience greater environmental variability (Berry et al., 2021; Starko et al., 2019, 2024), which is likely linked to RP1. In contrast, there is some evidence that wave exposed kelp forests in Western Australia have grown patchier than those in more sheltered areas over the past ~2 decades which spanned an unprecedented, ecosystem-transforming MHW (Mulders et al., 2022). In addition to mediating the impacts of MHWs on subtidal communities, wave action can also ameliorate the impacts of temperature on intertidal communities during low tide (Fitzhenry et al., 2004). Wave splash can cool down organisms that are exposed to hot air temperatures during summer low tides, potentially limiting their responses during atmospheric heatwaves (Hesketh & Harley, 2023) which can co-occur with MHWs (e.g., Starko et al., 2019; Whalen et al., 2023).

3.3 | Water chemistry and other environmental variables

There are several other environmental gradients with the potential to mediate MHW impacts, many of which are linked to water chemistry. There is strong evidence for interactions between temperature and salinity (e.g., Gegner et al., 2017; Kashenko & Korn, 2003), nutrients (e.g., DeCarlo et al., 2020; Fernández et al., 2020; Gerard, 1997), oxygen (e.g., Melzner et al., 2007), and pH (e.g., Hollarsmith et al., 2020) based on experiments measuring physiological performance of marine species. Thus, there is strong theoretical reasoning to expect local gradients in these variables to play key roles in mediating biological responses to MHWs. Environmental nutrients (especially nitrogen and phosphorous) can negatively impact the thermal tolerance of reef-building corals (DeCarlo et al., 2020), causing dysbiosis (Morris et al., 2019; i.e., RP3 acting on microbial communities to cause maladaptation of the host) and leading to increased prevalence of bleaching (Donovan et al., 2020; Vega Thurber et al., 2014). In contrast, for habitat-forming kelps, sufficient nutrients can increase thermal tolerance (Fernández et al., 2020; Gerard, 1997), suggesting that nutrient-rich regions may be more resistant to climatic stressors compared to comparable nutrient-poor regions (presumably through RP1). Similarly, salinity is known to influence the thermal tolerance of a range of marine taxa including crustaceans (e.g., Kashenko & Korn, 2003), cnidarians (e.g., Gegner et al., 2017), and seaweeds (e.g., Druehl, 1978). Interactions between temperature tolerance and salinity may become increasingly important in the future because climate change is expected to alter freshwater outflow and rainfall, potentially impacting the strength and distribution of salinity gradients across coastal ecosystems (Wikner & Andersson, 2012). Spatial variation in light can also mediate the impacts of MHWs. At Île Alphonse, Seychelles, corals that were shaded by leaf foliage in the lagoon fared better during the devastating 1997–1998 MHW than those on the outer reefs, despite the warmer temperatures experienced in the lagoon (Iluz et al., 2008). Moreover, turbidity and light limitation in New Zealand has exacerbated losses of giant kelp forests linked to a warming climate and MHWs (Tait et al., 2021).

3.4 | Anthropogenic disturbance

Anthropogenic disturbance describes a range of drivers associated with the presence of human populations along the coast (Halpern et al., 2015), including nutrients and turbidity from pollution, changes in salinity through alterations to freshwater outflow, and other disturbances such as trampling and dredging (Halpern et al., 2015; Watson et al., 2016). While fishing is not an environmental driver per se, the selective removal of certain species can be seen as a species filter that may cause similar impacts as RP3. Interactions between anthropogenic disturbance gradients and MHWs have received reasonable attention in the literature and can impact biological responses of MHWs through all three RPs (Table 1) (e.g., Bates et al., 2019; Baum et al., 2023; Darling et al., 2010; Starko et al., 2023). Variation in outcomes associated with interactions between anthropogenic disturbance and MHWs depends on the strength and characteristics of the underlying disturbance (Maucieri et al., 2023) as well as the characteristics of the MHW itself.

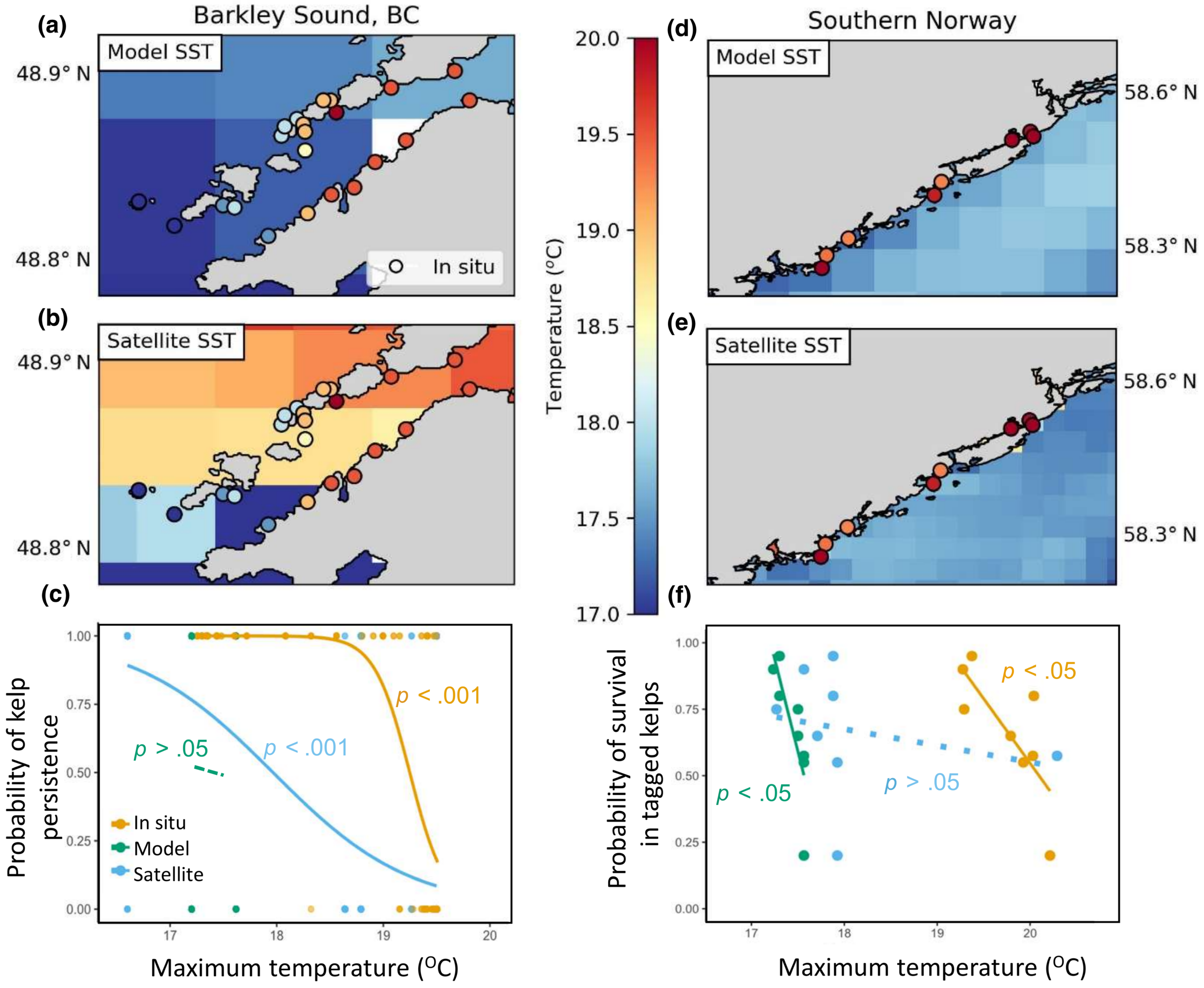

FIGURE 7 Local gradients in sea surface temperature (SST) and their effect on survival rates of kelp during a marine heatwave (MHW) for two case studies. The three left panels (a–c) show data from Barkley Sound, British Columbia, Canada adapted from Starko et al. (2022). Maximum sea surface temperature from June 22, 2019 until August 6, 2019 (during an MHW) are shown based on three methods (model; see below), satellite (see below), and in situ temperature loggers. (c) In situ and satellite temperatures are strongly predictive of changes in kelp distribution that occurred during an earlier MHW from 2014 to 2016. The right panels (d–f) show data from southern Norway, adapted from Filbee-Dexter et al. (2020). Maximum sea surface temperature from August 22, 2018 until October 15, 2018 are shown using the same methods. (f) In this case, modeled and in situ temperature both significantly predicted the mortality of individual tagged kelps. Modeled temperature data are from the E.U. Copernicus Marine Service Information (CMEMS) Global Ocean Physics Reanalysis (CMEMS MDS, accessed on March 2024) at 1/12° (~9 km) horizontal resolution and daily temporal resolution. Satellite temperatures are from MODIS-Aqua (NASA Ocean Biology Processing Group, accessed on March 2024) at 4 km horizontal resolution and daily temporal resolution. Circles in the top and middle panels show the in situ measured temperatures.

3.5 | Depth, elevation, and aspect

Bathymetric features such as depth, or tidal elevation (for intertidal ecosystems), and aspect can also create environmental gradients in a wide range of factors such as light, temperature, and nutrient availability. Depth has been long discussed as an important mediator of responses to environmental change (e.g., Bongaerts et al., 2010; Hughes & Tanner, 2000). Deep water refugia are arguably most well known in the context of coral reefs that can extend into the mesophotic zone (Bongaerts et al., 2010). Several studies have demonstrated reduced impacts of MHWs on coral reefs found at greater depths. However, this result has not been universal (Bruno et al., 2001; Hoegh-Guldberg & Salvat, 1995). There is now also strong evidence that the impacts of climate change may vary across depths in both kelp forests and seagrass meadows. For example, deeper kelp forests have been found to be more resistant to MHW events observed both in the Indian (Giraldo-Ospina et al., 2020) and Pacific (Ladah & Zertuche-González, 2004; Starko et al., 2022) Oceans. Deeper seagrass meadows were shown to fare better than shallower ones during the 2014–2016 Northeast Pacific MHW (Magel et al., 2022).

4 | LOCAL GRADIENTS AND INDIRECT EFFECTS

This review primarily focuses on the role that local environmental gradients play in driving responses to the direct effects of MHWs (i.e., warming of the ocean environment). However, local environmental gradients can also interact with indirect effects of MHWs. Heatwaves can alter the trophic structure of ecosystems (Rogers-Bennett & Catton, 2019; Vergés et al., 2016) or influence the prevalence or distribution of disease (Harvell et al., 2019). Local gradients can mediate these novel or changing interactions, potentially influencing emergent outcomes. Substrate properties can influence the efficiency of herbivory by benthic grazers (e.g., urchins) which can, in turn, influence the extent to which foundation species are impacted by these heatwave-induced trophic breakdowns (Randell et al., 2022; Starko et al., 2022). Local microclimates can also influence the susceptibility of species to disease during climate-mediated outbreaks. For example, local temperature conditions strongly predicted mortality of sea stars during the sea star wasting disease epidemic that coincided with the 2014–2016 Northeast Pacific MHW (Harvell et al., 2019; Miner et al., 2018). Overall, while this review focuses on the interplay between local gradients and direct effects of warming, local conditions can also play critical roles in determining indirect responses to MHWs.

5 | INCORPORATING LOCAL GRADIENTS TO IMPROVE UNDERSTANDING AND MANAGEMENT OF ECOSYSTEMS

To fully understand how more frequent and intense MHWs will impact species and ecosystems, it is essential to incorporate knowledge of fine-scale local variation. Indeed, the importance of local gradients in driving species' responses to climate change has been well documented in the literature on terrestrial taxa (e.g., Maclean et al., 2015; Suggitt et al., 2018) but this kind of local-scale variation is often ignored in marine systems (Bates et al., 2018). While some coastlines may be more homogenous than others in terms of the local gradients discussed above, these gradients are ubiquitous in the coastal ocean. Although predicting (through modeling) or interpreting (through observation) conditions during MHWs at scales fine enough to fully capture this variation requires well-resolved environmental data, these data likely do not exist for many regions (Li Shing Huing et al., 2024; Reese, 2023). However, recent advancements—for example, in monitoring programs (Li Shing Huing et al., 2024; Reese, 2023), remote sensing platforms (e.g., Wachmann et al., 2024), climate models (Fatland et al., 2016), ecological genomics (Smith et al., 2022), and open data (Klein et al., 2017; Li Shing Huing et al., 2024)—provide an opportunity to fill some of these data gaps.

The rise of large-scale programs that are capturing fine-scale local environmental variation suggest that this kind of monitoring is possible (Li Shing Huing et al., 2024; Reese, 2023) and provides an opportunity to expand these environmental programs in other systems. These programs are facilitated in part through improvements in the accuracy, reliability, and battery life of in situ data loggers in recent years (e.g., ElectricBlue), with numerous options now available to record temperature and salinity every hour for a year or more before requiring servicing. Actions should be prioritized to support similar developments for other variables identified in the sections above.

Where in situ measurement is difficult, remote sensing technologies that facilitate fine-scale characterization of environmental variables, such as thermal bands from high-resolution satellites or predictions from ocean forecasting models, are likely to offer a promising way forward. Satellite and other remote sensing technologies continue to improve in the number of essential variables they can detect and in their spatial and temporal resolution (Cavanaugh et al., 2021). For example, recent work suggests that LandSat thermal bands (with a resolution of 30 m, compared to 1–4 km with MODIS) that have been collecting data since the 1980s may provide an important tool for quantifying local-scale gradients in sea surface temperature (Wachmann et al., 2024). Similar advancements in the development of ocean models also offer an ever-improving view of environmental heterogeneity across the coast (e.g., Fatland et al., 2016).

Importantly, at present, both key satellite (MODIS) and modeling (Copernicus) approaches have the potential to capture some key gradients at the scale of a few kilometers (e.g., Figure 7) but may provide a biased measure of absolute temperatures or be inconsistent. For example, in the case studies presented in Figure 7, modeled sea surface temperature (SST) fails to capture the thermal gradient in Barkley Sound (Figure 7a,b) that is clear in satellite and in situ data. In contrast, modeled SST captures the thermal gradient in Southern Norway (Figure 7d) but suggests that maximum temperatures are several degrees cooler than those observed in situ. Similarly, several of the case studies we describe in this review reflect gradients present at a finer scale than readily available satellite and modeling products (Table 1). Open data platforms and networks (e.g., through the many integrated ocean observing systems coming online) will also help ensure these fine-scale data are available in near real time to managers and policymakers.

In addition to remote sensing and modeling, observational and experimental studies alike should work to enhance our understanding about how local-scale gradients are likely to impact species and ecosystems. While there are numerous experiments documenting complex interactions between temperature and co-occurring factors such as salinity, nutrients, aerial immersion, light levels, and water motion (Bonacina et al., 2022; Hollarsmith et al., 2020; Takolander et al., 2017), more work is required to identify key thresholds and to strategically characterize the nature of these interactions such that they can be incorporated into both the analysis of monitoring data and predictions of future change. The adaptive capacity of species and the extent to which phenotypic variation develops across local gradients remain an emerging area of research and for which modern genomic approaches offer key insight (e.g., Palumbi et al., 2014). Moreover, linking local-scale phenotypic variation to environmental variation occurring during MHWs remains a key area for future study. While a small number of experiments or case studies may point to increased MHW resistance in warm-adapted populations, outcomes in this scenario are likely to be highly variable, calling for improvements in both theoretical and empirical approaches to understanding these systems.

Critics may argue that focusing on such fine-scale local gradients might be overly costly or challenging, yet a failure to assess the impacts of MHWs at the appropriate spatial scale may have negative conservation implications. By ignoring local gradients, scientists may under- or overestimate the risk of future heatwaves toward a particular ecosystem, thereby mis-directing limited resources, or reducing the time available to policymakers and managers to act. Similarly, ignoring local-scale factors could lead scientists to miss early warning signs of population declines (e.g., Cowlishaw et al., 2008) which are often needed to trigger protections through species-at-risk legislation. These protections often mandate targeted management actions such as designation of critical habitat or the identification and management of competing anthropogenic stressors described above, interventions which could mean the difference between extirpation and persistence. Indeed, it is at the fine scales of these local gradients that most conservation and restoration action takes place (Eger et al., 2023; Helmuth et al., 2014; Wood et al., 2024). Thus, understanding how MHWs and other climate change-driven phenomena interact with local gradients will be essential for ensuring ecosystem resilience into the future.

6 | CONCLUSIONS

As climate change continues to alter the distribution of species and the dynamics of our ocean ecosystems, we must work to understand and predict variability in the responses of species and ecosystems. Fine-scale environmental gradients offer an important lens through which to assess this variability. Impacts of climate change may be partially or entirely contingent on the pre-existing conditions in a particular locality and these conditions can vary on the scale of kilometers, meters, or even centimeters. We present a simple framework which relates the mediating impacts of local gradients during MHWs to modern ecological theory. We then linked the components of this framework to real-world case studies. Finally, we discuss how future technologies and continued on-the-ground research will be essential to better integrate local gradients into our predictions and interpretation of climate change impacts. If we are to accurately interpret and predict the ways that climate change is altering the ocean environment, we must better understand both the way that local gradients are distributed across the coast and how they will interact with extreme climatic events to shape future ecosystems.

AUTHOR CONTRIBUTIONS

Samuel Starko: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; visualization; writing – original draft; writing – review and editing. **Mirjam van der Mheen:** Data curation; formal analysis; investigation; methodology; visualization; writing – original draft; writing – review and editing. **Albert Pessarrodona:** Investigation; methodology; writing – original draft; writing – review and editing. **Georgina V. Wood:** Investigation; methodology; writing – original draft; writing – review and editing. **Karen Filbee-Dexter:** Investigation; methodology; writing – review and editing. **Christopher J. Neufeld:** Conceptualization; writing – original draft; writing – review and editing. **Shinae Montie:** Data curation; investigation; methodology; writing – review and editing. **Melinda A. Coleman:** Investigation; supervision; writing – review and editing. **Thomas Wernberg:** Investigation; supervision; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data are available in the manuscript or at https://doi.org/10.5281/zenodo.13183818.

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