Temperature extremes in the Gulf of Maine: A synthesis of marine heatwaves, cold-spells, and ecological impacts

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Abstract

Long-term environmental change has been altering ecosystem function and phenology globally. Short-term temperature pulses, often called extreme temperature events, can accelerate impacts of long-term change on ecosystems by forcing rapid changes in food webs, triggering range shifts, and disrupting reproductive cycles. Marine ecosystems at the confluence of large global currents are particularly vulnerable to extreme temperature events because small shifts in currents can trigger rapid local change. The Gulf of Maine, located at the confluence of the Labrador Current and the Gulf Stream, is one such marine ecosystem. The Gulf of Maine has experienced rapid warming in recent decades, punctuated by frequent extreme temperature events which have impacted productive fisheries and diverse ecosystems in the region. Yet, synthesis work has not quantified changes in extreme temperature events over time or the implications for Gulf of Maine ecosystems. From 1993 to 2025, we observed a 3% yearly increase in marine heatwave events with a 4% yearly decrease in marine cold-spells, but trends varied spatially across the Gulf of Maine. To assess how these events are impacting Gulf of Maine ecosystems, we conducted a formal literature review. Here, we identified 12 papers (from a search of 539 that met our initial criteria) that focused on extreme temperature events affecting ecosystems in the Gulf of Maine; this dearth of papers highlighted the need for more work in the region. Across marine ecosystems, we noted the direct physiological impacts of extreme events, as well as the cascading effects these events cause by enabling the spread of disease, altering food webs, and disrupting fisheries. We also reviewed how extreme events affect coastal human communities and how this might change in the future with emerging stressors and human migration. Lastly, we pointed out research gaps, especially in relation to designing management plans that account for extreme events.

Impact Statement

We couple an analysis of long-term trends in extreme temperature events with a literature review of their impacts on marine ecosystems in the Gulf of Maine. We demonstrate that there has been a limited amount of work in the region on temperature extreme events compared to work on warming more generally. We identify emergent themes of species- to community-level impacts and highlight important research gaps for future work. Given the Gulf of Maine's rapid warming, we aim for this work to chart a path for managers and other scientists in regions where the impacts of warming are increasingly observed.

Keywords: Gulf of Maine; marine heatwaves; extreme events; marine ecosystems; press and pulse; disturbance

1. Introduction

Large-scale thermodynamic changes are altering interconnected processes across terrestrial and aquatic systems, contributing to an increased frequency and intensity of extreme events, including heatwaves, cold-spells, heavy precipitation, and damaging winds (Easterling et al., 2000; Fischer et al., 2025; Robinson et al., 2021). Against the backdrop of climate change as a long-term "press" disturbance, extreme events are "pulses" that can trigger rapid ecological responses, particularly when they occur more frequently or interact with ongoing environmental change (Harris et al., 2018). Among extreme climatic events, temperature extremes are especially consequential as they can impose acute physiological stress on a wide range of taxa, affecting their metabolic performance, behavior, reproduction, and survival (Angilletta Jr, 2009). Further, these events can have cascading effects such as mass mortality of dominant species leading to dramatically altered ecosystem function or regime shifts (Bréda et al., 2006; Hughes et al., 2018; Ruthrof et al., 2018; Wernberg et al., 2013). Thus, as once-rare extremes are projected to become commonplace, understanding direct ecological impacts of extreme temperature events is both critical and urgent (Davariashtiyani et al., 2023; Fischer et al., 2025; Intergovernmental Panel on Climate Change (IPCC), 2023; Murali et al., 2023).

Temperature extremes have strong impacts on marine ecosystems, including mass mortality events, reproductive failure, low recruitment, and range shifts for native and non-native species (Hartog et al., 2023; Kress et al., 2017; Schlegel et al., 2021; Shanks & Brundage, 2013; Wernberg et al., 2013). While various criteria have been used to define marine temperature extremes (Ummenhofer & Meehl, 2017), Hobday et al. (2016) presented a standard definition for marine heatwaves (MHWs) that is broadly used today; a standard definition for marine cold-spells (MCSs) has followed suit (Schlegel et al., 2021). Globally, MHWs have risen in frequency (34%), duration (17%), and intensity (varying) over the past century (Oliver et al., 2018). As such, literature on this topic has substantially increased over the last decade (Bass et al., 2021; Hartog et al., 2023; Oliver et al., 2021). By contrast, MCSs have declined across most ocean surfaces over the last 40 years (Frazer et al., 2026; Schlegel et al., 2021). Consequently, they have received less attention and categorization than MHWs, even though they can have similarly adverse ecological impacts (Schlegel et al., 2021).

MHW and MCS events are especially relevant in the Gulf of Maine (GoM), a semi-enclosed sea bordered by the coastlines of Massachusetts, New Hampshire, Maine, New Brunswick, and Nova Scotia. The GoM is one of the fastest-warming large marine ecosystems in the world, with continued warming of sea temperatures of 1.1 to 2.4 °C projected under future climate scenarios (Brickman et al., 2021; A. J. Pershing et al., 2021). Warming projections are concerning because the GoM is a highly productive and ecologically diverse marine system that supports both complex ecosystems and coastal human communities (Thompson, 2010). Spanning approximately 93,000 km^2 and encompassing 12,000 km of coastline and islands, the region includes a mosaic of habitats such as estuaries, rocky intertidal zones, and a large, offshore pelagic area (Thompson, 2010). The GoM is also oceanographically distinct, shaped by the interaction of cold, nutrient-rich Labrador slope waters and warmer, lower-nutrient Gulf Stream waters, which together regulate primary productivity and structure food webs at the base of the ecosystem (Switzer et al., 2020). These ecosystems support a major marine economy centered around commercial fisheries, tourism, and recreation, with more than two-thirds of the region's population living along the coastline and relying on functioning coastal systems that contribute substantially to human well-being (Thompson, 2010). Extreme events may disproportionately impact those who rely on the GoM's natural resources, such as the Mi'kmaq peoples in Nova Scotia who are underrepresented in fisheries management decisions despite their established right to these resources (Elegbede et al., 2023). Consequently, both long-term climatic shifts and acute temperature extremes are expected to have increasingly profound effects across the GoM's interconnected ecosystems and human communities.

Despite increasing recognition of extreme temperature events as key drivers of ecological change and socioeconomic disruptions in the GoM, research has largely focused on singular, high-profile disturbances (e.g., the 2012 MHW) rather than adopting a comprehensive view of these events (Bricknell et al., 2021; K. E. Mills et al., 2013; A. J. Pershing et al., 2015; D. W. Townsend et al., 2023). This has resulted in a fragmented understanding of how MHWs and MCSs influence marine ecosystems. Moreover, comparatively little attention has been given to cold temperature extremes, despite their potential to impose equally strong physiological and ecological constraints (Wasson et al., 2025). As a result, there remains a critical need to synthesize the impacts of temperature extremes on GoM ecosystems and the human communities that depend on them.

We address these knowledge gaps by synthesizing our current understanding of temperature extremes in the GoM with a focus on MHWs and MCSs (Fig. 1). Specifically, we quantify recent trends in temperature extremes using long-term environmental datasets; review the direct effects of MHWs and MCSs on marine organisms across taxa; examine indirect and cascading impacts, including trophic interactions, feedback loops, and implications for ecosystem function and fisheries; and identify the key gaps in the literature to guide future research and management. By integrating across event types and ecological scales, this synthesis aims to provide a more comprehensive framework for understanding how extreme temperature events are reshaping one of the world's more rapidly changing marine ecosystems.

2. Long-term temperature trends

We analyzed extreme temperature events in the GoM by evaluating long-term, publicly available temperature time series at two oceanographical scales: A large scale, averaging temperature measurements for the whole GoM, and a local scale, extracting locally sourced buoy temperature data. We detected MHWs and MCSs using the R package *heatwaveR* version 0.5.5 (R Core Team, 2020; Schlegel & Smit, 2018), which implements Hobday et al. (2016)'s definition for MHW and MCSs. First, we used an 11-day moving average window to define the climatological baseline. Based on the climatological baseline, we calculated the 90th and 10th percentile thresholds for the extent of each time series. An MHW or MCS was declared each time one of these thresholds (either above the 90th percentile for an MHW or below the 10th percentile for an MCS) was exceeded for five or more consecutive days. We then recorded the number of events or number of total number of days per year above these thresholds.

For the large-scale analysis, we downloaded SST data from the European Union Copernicus Marine Service Information portal using the package CopernicusMarine v. 0.2.2. (de Vries, 2023) for R. Copernicus provides daily, gap-free modeled environmental data with a resolution of 1/12°. We constrained variables to the study region using the approximate boundaries of the GoM (-72° W, -62° W, 46°N, 39° N, according to the U.S. maritime boundary for the GoM). We downloaded data from January 1993 to December 2024. We calculated mean daily and yearly temperature values by averaging pixel values within each grid.

For the local, *in situ* measurements of temperature, we downloaded data from NOAA's National Data Buoy Center (NDBC) using the buoydata package in R. We filtered the buoys within the boundary of the GoM from the buoy data catalog. Since buoy data contains temporal and spatial gaps in temperature measurements, we screened our datasets using the criteria presented in Schlegel & Smit, 2018 and our Appendix.

For the GoM-wide analysis, we found that SST values showed a significant increase throughout the years (p<0.001). We observed a significant increase in the annual count of extreme SST events across the GoM (rate ratio=1.03, p=0.03), while MCS events decreased (rate ratio=0.96, p=0.04) (Figs. 2, S1).

For the local-scale buoy analysis, MHW days generally increased, while MCS days decreased across the buoys that met our selection criteria (Figs. 2, S2). These results are in line with the expected trends of increasing MHW days (Oliver et al., 2018). Significant increases in MHW days per year were present in one-third of buoys, while significant decreases in MHW days were present in one-sixth of buoys (Tables S1, S2, S3). However, all buoys with greater than 40 years of data experienced a significant increase in MHW days over time. Half of the buoys had positive trends in annual MHW events per year, and eleven buoys presented negative trends in the annual occurrence of MCS events per year.

3. Literature Review

We conducted a literature review with the goals of characterizing the current literature on ecological impacts of extreme temperature events in the GoM and identifying knowledge gaps. We systematically searched the Scopus database using 45 search terms (Appendix), identifying 539 results. We then filtered the results to select only field-based studies examining the ecological impacts of extreme temperature events in the GoM (see Appendix for detailed methods). Ultimately, 12 papers met our review criteria (Table 1).

Of the papers selected for review, 11 examined the ecological impacts of MHWs, and one described the impact of an MCS. In addition to describing a distinct type of event, the MCS paper was older than the rest. In fact, the described MCS occurred in the early 19th century, whereas the described MHWs occurred over the last three decades (Fig. 3, Table S3). The focus of recent literature on MHWs aligns with our finding that MHW frequency has significantly increased in recent years, whereas MCS frequency has declined (Fig. S1).

Collectively, the reviewed studies encompassed a broad range of taxa and geographic scales across the GoM. MHW impacts were documented in mollusks, echinoderms, arthropods, birds, and fish (Fig. S4). Study sites were well distributed throughout the GoM, spanning a range of latitudes and distances from the coast. Some studies were focused on highly localized systems (e.g., Barber et al. 1997, Scheibling & Hennigar 1997), whereas others examined impacts to the entire GoM (e.g., Pershing et al. 2018) or included the region as part of a broader discussion of the U.S. Eastern Seaboard (e.g., Diamond et al. 2020).

We found that of the reviewed studies, only one-third described physiological impacts of extreme temperatures. Two-thirds of studies documented ecosystem-wide impacts of extreme temperature events, which appeared to have resulted from temperature-induced trophic and epidemiological shifts rather than direct thermal stress. Causal links between extreme temperature events and ecological impacts are difficult to provide due to the opportunistic nature of field data collection and the transient quality of the events in question (Altwegg et al., 2017; Bailey & van de Pol, 2016). Nevertheless, our review identified strong *in situ* evidence for four categories of ecological impacts: physiological and phenological impacts, disease events, trophic shifts, and changes in human activity.

4. Impact Themes

4a. Physiological and phenological impacts

All reviewed studies documenting physiological and phenological impacts of extreme temperature events reported changes in spawning, recruitment, or larval development, indicating that reproduction and early life stages are particularly vulnerable to both MHWs and MCSs. For example, Runge et al. (2015) documented reduced egg production and delays in diapause in an ecologically important copepod species during an MHW. Similarly, Alexander et al. (2017) described GoM-wide impacts on spawning, egg, larval, and juvenile fish survival during the volcanic winter of 1815. Pelagic fish populations persisted, likely because they were adapted to spawning in colder temperatures, while alewife populations declined in response to unfavorable temperature fluctuations during the time of spawning.

Organisms have adapted to specific thermal windows which govern their spatial distributions, and in some cases, MHWs altered species distributions. During MHW events in 1952, 1990, and 2012, the northern edge of the lady crab's (*Ovalipes ocellatus*) range shifted into the GoM (Johnson et al., 2025). Persistent warming around 2012 (Figs. 1, 2) may have enabled this relatively warm-adapted lady crab to establish a permanent population in the GoM in the last decade (Johnson et al., 2025). Our analysis supports Johnson et al.'s hypothesis that broader warming trends have increased the frequency of MHWs (Figs. 1,2), creating conditions that potentially facilitated lady crab's range expansion to the GoM.

Species' thermal preferences may vary between their life stages, enabling cold-adapted species to benefit from MHWs during specific reproductive and developmental stages. For example, two stickleback species at the southern edge of their range experienced enhanced reproductive success during the 2012 MHW (McCleave et al., 2018). Anomalously warm spring temperatures promoted earlier spawning and reduced overwinter mortality, resulting in increased stickleback abundance the following year. The 2012 MHW was particularly long in duration, with several sites across the GoM experiencing a large number of extreme event days (Figs. 1,2, Table S1, S2), providing prolonged favorable conditions that likely contributed to these population increases (McCleave et al. 2018). Extreme temperature events may also influence organisms indirectly by producing secondary environmental changes that impact physiology. For example, MCSs can cause extreme ice scour events which physically crush or scrape away intertidal organisms (Box 1).

4b. Disease events

Two of the papers reviewed here documented disease-related mass mortality events following MHWs. Sea urchin populations along the Atlantic coast of Nova Scotia declined to near local extinction following an anomalously warm summer in 1995 (Scheibling & Hennigar, 1997). Disease incidence subsided as temperatures dropped in the fall, but the authors hypothesized that future temperature anomalies could produce recurring disease outbreaks, possibly forcing a successional shift from urchin barrens to kelp forests (Scheibling & Hennigar, 1997). MHW conditions also seem to have facilitated the introduction of the oyster pathogen MSX into wild oyster reefs in Great Bay, New Hampshire, in the fall of 1995 (Barber et al., 1997). In addition to being anomalously warm, 1995 was the driest year in a decade; the combination of warm and high salinity conditions likely allowed MSX to establish itself in New Hampshire that year (Barber et al., 1997). In both studies, disease events are contingent on seasonal temperature cycles, suggesting that the increasing frequency of summer MHWs may intensify future disease outbreaks.

4c. Trophic shifts

MHWs can alter the spatial distributions of predators and prey, disrupting food webs and leading to impacts ranging from mass starvation to mass mortality. Atlantic puffins provide a striking example of predator response to extreme events. During GoM MHWs over the past decade, puffins experienced declines in their preferred prey availability and, despite turning to lower-quality alternative prey (Kennerley et al., 2024), starved e*n masse* (Diamond et al., 2020). Low prey availability affected both juveniles and adults: juveniles required more time to reach maturity, while adults spent more time foraging (Wallace et al., 2025). Diamond et al. (2020) hypothesized that the summer of 2012 starvation event forced seabirds to leave the GoM in search of prey. Further, their depleted energy reserves left them vulnerable to subsequent weather events, resulting in the unprecedented puffin and razorbill auk wrecks in both Cape Cod and Florida during the winters of 2012 and 2013.

Heatwave-induced range shifts can also increase predation pressure and drive mass mortality among prey species. For example, increased predation was likely responsible for the collapse of the GoM northern shrimp population following the 2012 MHW (Richards & Hunter, 2021). Richards and Hunter (2021) found that several northern shrimp predators expanded their ranges into the GoM during the heatwave, with longfin squid likely exerting the greatest impact because of their particularly rapid range expansion (Richards and Hunter 2021). The authors suggested that longfin squids' short life cycles may have accelerated the speed of their invasion into the GoM. Together, these studies demonstrate that trophic impacts are a common consequence of extreme temperature events and often arise as indirect effects of temperature-driven changes in species physiology, phenology, and distributions.

The dramatic food web impacts of the 2012 MHW exemplify how prolonged, high-intensity summer MHWs can trigger cascading ecosystem-wide effects. Our analysis supported that the 2012 MHW was indeed unusually long and intense. It further showed that MHW frequency has continued to increase, suggesting that similar severe events may occur more often if current warming trends persist (Figs. 2, S1).

4d. Changes in human activity

The GoM hosts the highest value fishery in the USA (NOAA Fisheries, 2026). Extreme temperature-driven changes in species distributions and abundance have often caused significant economic shocks to fisheries in the region. The reviewed studies illustrate both successful and unsuccessful examples of fisheries' adaptive capacity. Following the cold-spell-induced collapse of the alewife fishery in 1815, the GoM fishery shifted its focus to mackerel, a species which benefited from the colder temperatures (Alexander et al., 2017). This shift reduced fishing pressures on alewives, allowing populations to recover and demonstrate one successful example of an adaptation to an extreme temperature event (Alexander et al., 2017). Conversely, industry infrastructure was unprepared to manage the surge in lobster landings during the 2012 MHW (K.

Mills et al., 2017). Landings exceeded both processing capacity and market demand, causing lobster prices to drop dramatically (Mills et al., 2017; Pershing et al., 2018). In response, Mills et al. (2017) attempted to help communities adapt to future MHWs by developing a lobster landing forecast. Although the impacts of this forecast on the industry during the similarly intense 2016 MHW were unclear, expanded Maine lobster advertising following 2012 likely helped 2016 prices remain stable (Pershing et al., 2018). Adaptive strategies for fishery booms and busts are very different, but the papers reviewed here provide a few examples of successful human adaptation to extreme temperature event impacts on the GoM fishery.

5. 2012 MHW event and implications for MHW literature

More than half of the papers in our literature review discuss the impacts of the 2012 summer MHW (Table 1). For five of our 13 buoys, 2012 was the year with the most MHW days, reaching maximum intensities from 1.7 °C to 5.2 °C above climatological baseline temperatures at those sites (Tables S1, S2). The 2012 MHW sits in a definitional gray area; while the multi-season-long duration of this event may indicate that it is more a signal of long-term warming than an extreme event, we opted to include papers discussing this event in our review.

The 2012 MHW exemplified how physiological impacts can create trophic cascades. The event caused American lobster populations to boom, likely because the temperatures were beneficial for lobster reproduction and larval development (K. Mills et al., 2017; A. Pershing et al., 2018), alongside several other predator species (Richards & Hunter, 2021). Increases in predation caused a rapid decline in northern shrimp populations (Richards & Hunter, 2021), and declines in these low-trophic-level species led to starvation and later strandings among seabird populations (Diamond et al., 2020). Rapid changes in American lobster and northern shrimp availability caused lobster prices to plummet, an economic event which left GoM fishermen reeling for years (K. Mills et al., 2017). While our literature review primarily focused on the 2012 MHW's impacts on a small subset of species of commercial importance, the overarching narrative is one of secondary, tertiary, and quaternary impacts on a highly connected ecosystem. We would hypothesize that this event reached less well-studied species in addition to those documented in our review.

MHWs that exceed even the new, warming baseline—such as 2012—may be the most dangerous. For example, our data analysis suggested that the 2021 MHW was similarly long and intense to the 2012 event, surpassing 2012 as the year with the most MHW days in our analysis of the GoM-wide satellite data (Tables S1, S2). However, only one paper in our literature review discussed impacts from the 2021 event (Wallace et al., 2025), and this lack of papers may be due to a multi-year lag between event occurrence and publication. The seven papers on the 2012 event were published between three and 13 years after the MHW, with a mean lag in publication time of seven years. Thus, we hypothesize that the 2021 MHW likely also caused diverse, cascading impacts on understudied trophic interactions, reproduction and physiology, and range expansion. However, new, range-expanding species, causal disease agents, and prey for species of commercial interest may emerge in the GoM MHW literature as researchers seek to understand the mechanisms behind the 2012 MHW's impacts on well-monitored species.

6. Research and Management Priorities

In the following sections, we outline our recommendations for research and management actions to improve our understanding of and response to extreme temperature event impacts in the GoM. While these recommendations are grounded in our findings from the GoM region, they may be relevant to other rapidly changing ecosystems.

6a. Provide a clear definition for extreme temperature events

Definitions of extreme events are built from historical climatological baselines (Bailey & van de Pol, 2016; Hobday et al., 2016). For our detection of trends, we used a standard definition for MHWs (Hobday et al. 2016) with a similar standard definition for MCSs (Schlegel et al., 2021). This definition examines daily 90th and 10th percentile thresholds based on a fixed climatological baseline, which, if exceeded for five or more consecutive days, is classified as an extreme temperature event.

Of the twelve papers in our literature review, only three explicitly used Hobday et al. (2016)'s definition. Among the papers that did not reference Hobday et al. (2016)'s definition, six calculated temperature anomalies from *in situ* temperature data, and three cited anomalous temperature conditions but did not provide the associated analysis (Table S3). Part of the challenge in comparing across systems and types of extreme events is the lack of consistent definitions of extremity (as seen in our literature review) and the sensitivity of MHW and MCS detection to the choice of climatological baseline (Amaya et al., 2023; Giménez et al., 2024; Smith et al., 2024; Jacox 2019).

For extreme temperature events, other considerations of the temperature regime, including duration, extent, and cumulative exposure (Whitaker & DeCarlo, 2024; Zhao et al., 2026), as well as biologically based definitions are needed (Özcan et al., 2026; Villeneuve & White, 2025). For example, biological definitions of extremity may suit studies of organismal physiology best, while climatological baselines that update with warming may help define MHWs relevant to rapidly adapting or range-expanding organisms. Future work to describe the impacts of extreme temperature events in the GoM should provide a clear description of the methodology used to confirm the presence of an extreme event and a justification for the methodology used, informed by the study's research questions.

6b. Explore potential compounding impacts of repeat extreme events

Most of the impacts described in our literature review focus on single events. Yet, compound thermal events may become increasingly important (AghaKouchak et al., 2020). For example, the timing between extreme events affects whether a system can respond adequately for coral reefs and forest fires (Dalton et al., 2020; Zhang et al., 2024). The same is true for how human societies respond to extreme events and corresponding feedback loops (White & Wulfing, 2024). In addition, thermal extremes interact with other stressors—stratification, eutrophication, and invasive species—to generate multi-stressor events. For example, elevated temperatures enhance microbial metabolism and oxygen demand, reinforcing feedback loops that favor hypoxia and algal blooms. Increasing SST variance and shortened recovery intervals are early warning indicators of declining resilience (Bernhardt, 2020). In the GoM, MHWs have evolved from episodic anomalies into structural drivers of ecological reorganization and socioeconomic instability. Our ice scour review also highlighted the multi-stressor nature of MCSs (Box 1).

6c. Integrate studies of extreme event impacts across species

Our work emphasized the overall dearth of studies focused on temperature extremes, as opposed to general warming trends or disturbances generally, in the GoM. Given the small sample size of papers that met our criteria, there is certainly room for bias in the papers we reviewed, but more broadly, the focus of research in general. Our review found most papers focused on particular well-known events, such as the 2012 MHW. Our data analysis suggested additional periods of MHW and MCS where ecological impacts may have occurred (Figs. 2, S1), but the ecological impacts of these extreme events are not represented in the literature. Further, a plurality of studies we reviewed focused on shellfish. This focus could be driven by more impacts on shellfish given the lack of mobility for many species and overall thermal sensitivity (Masanja et al., 2024). Alternatively, shellfish may be overly represented because they are easier to survey or because of their commercial value. More broadly, additional work is needed to understand if our trends are general or a function of bias in sampling and species coverage (Bennett et al., 2014; Fournier et al., 2019).

6d. Build short-term forecasts

Our review highlighted that most assessments of thermal events are conducted *post-mortem* (though see Mills et al., 2017), long after the event has taken place and impacts have already occurred. Future work could focus on building short-term forecasts, including the use of digital twins and other models, to project upcoming extreme thermal events (Brodie et al., 2023). These types of tools are needed for managers, scientists, business owners, and the public to respond in real-time. For example, shellfish farmers could move cages to deeper waters, use shading, or change harvest timing if given notice about upcoming MHWs (Hartog et al., 2023). This could build on examples like NOAA's Coral Reef Watch (Liu et al., 2006) by incorporating more information on species biology and local conditions (Villeneuve et al., 2026; Villeneuve & White, 2025). To achieve such goals, there would need to be concentrated effort to better understand specific species' thermal biology and deploy real-time environmental and biological sensors, which would be combined in forecasting and management products.

6e. Manage on an ecosystem level

Extreme events are complex ecological disturbances that have implications for social-ecological systems management and adaptive capacity (White & Wulfing, 2024). With rapidly changing ocean conditions in the GoM, continuous data monitoring and forecasting by state and federal management agencies are essential to inform management decisions in a timely manner (Waller & Staudinger, 2026). Current fishery management systems may not incorporate extreme temperature events due to their increasing frequency and a mismatch in the timeline for decision-making, which occurs at a slower pace (Golden et al., 2024; Hartog et al., 2023). This is reflected in broader literature on similar natural disasters where the timing between extreme events is now shorter than agencies' ability to learn from one event to prepare for the next (Huning & Brunner, 2026). Nonetheless, ecosystem-based management is an approach that incorporates the diversity of interactions between fisheries, climate, habitat, and human dimensions and can help operationalize management (Townsend et al., 2019).

7. Conclusions

We found an increase in MHWs and a decrease in MCSs over time in the GoM, but there were meaningful differences between subregions of the gulf. Our literature review revealed only a few papers on the impacts of thermal extreme events in the GoM with disproportionate focus on species of commercial interest and single, large MHW events (Tables S1, S2). We see our work as a foundation for future studies that: 1) clarify and use consistent definitions of extreme events; 2) explore effects of compounding and interacting extreme events; 3) improve monitoring and build short-term forecasts; and 4) and manage on the ecosystem level. We also believe that considering mechanisms for decreasing lag time between extreme temperature events and publication, e.g., popularizing shorter scientific notes in this subject, will speed up the adaptive management process.

Given the speed of change in the GoM, the area may prove to be a sentinel for other regions that are also undergoing changing extreme event regimes. Our work highlights the dearth of research on extreme temperature events specifically compared to overall warming. Our combined analysis and literature review approach helps identify events with documented impacts and events where impacts either did not occur or were not documented in the literature.

Data availability statement. All data used in this study are publicly available from NOAA's National Data Buoy Center (NDBC) and the European Union Copernicus Marine Service Information portal (Copernicus Marine). We included our code and data on GitHub https://github.com/QuantMarineEcoLab/gulfmaine_extremeevents

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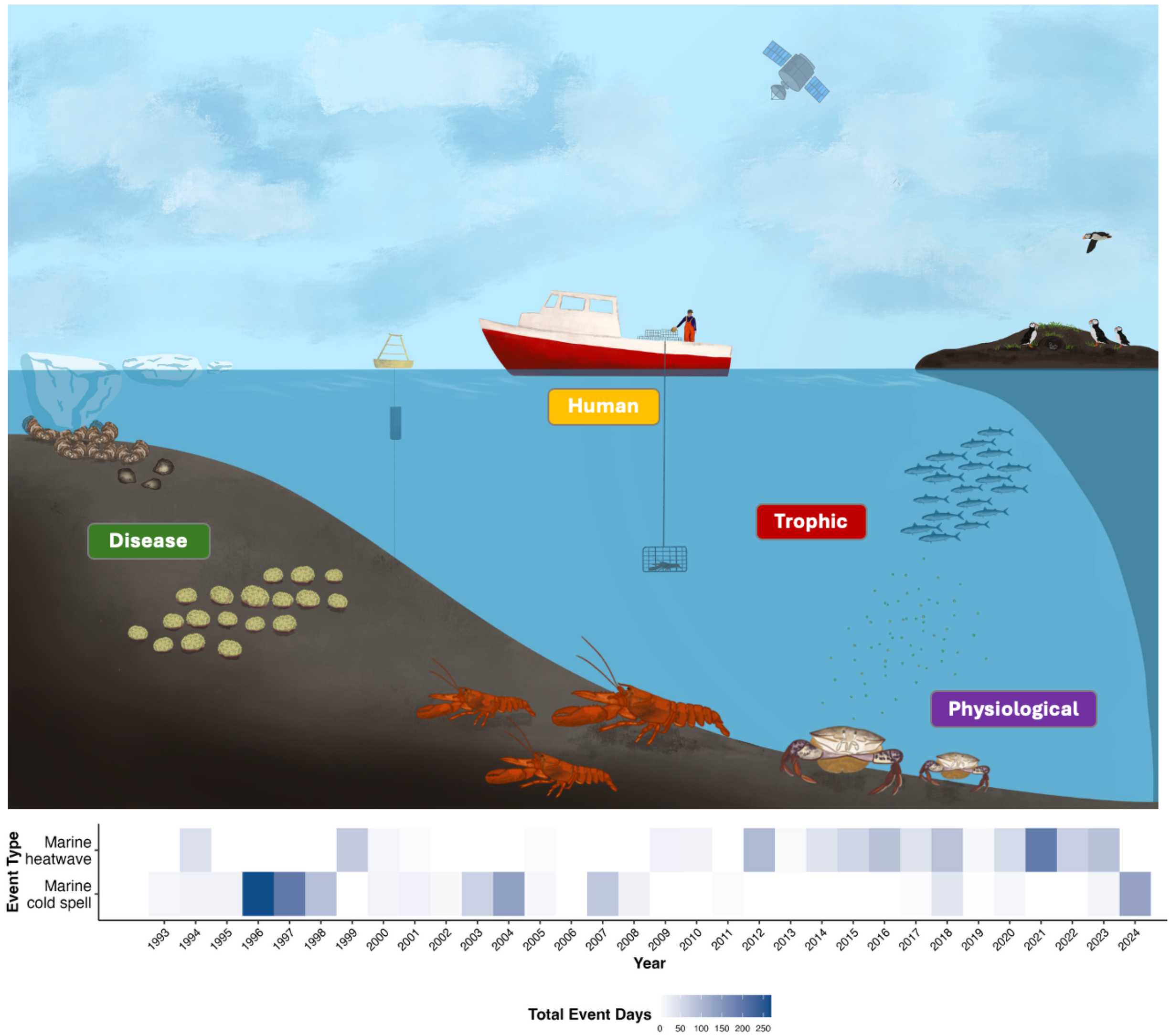


Figure 1. (Top) Impacts of Extreme Temperature Events on the GoM system. Long-term monitoring of temperature in the GoM using various technologies (e.g., satellites and *in situ* sensors) has allowed us to track changes in the frequency and intensity of extreme temperature events. These events affect the GoM system in numerous ways. MHWs have been associated with physiological and phenological changes (e.g., delayed egg production in copepod species), trophic shifts (e.g., changes in prey availability leading to a decline in puffin populations), and increased disease events (e.g., MSX in oysters). In turn, all ofthesecan affect human use of GoM resources (e.g., shift harvest timing). (Bottom) Annually, the total number of days classified as marine heatwaves (MHWs) has increased, while the total number of days classified as marine cold-spells (MCSs) has decreased. Annual trends are depicted using GOM-wide SST data.

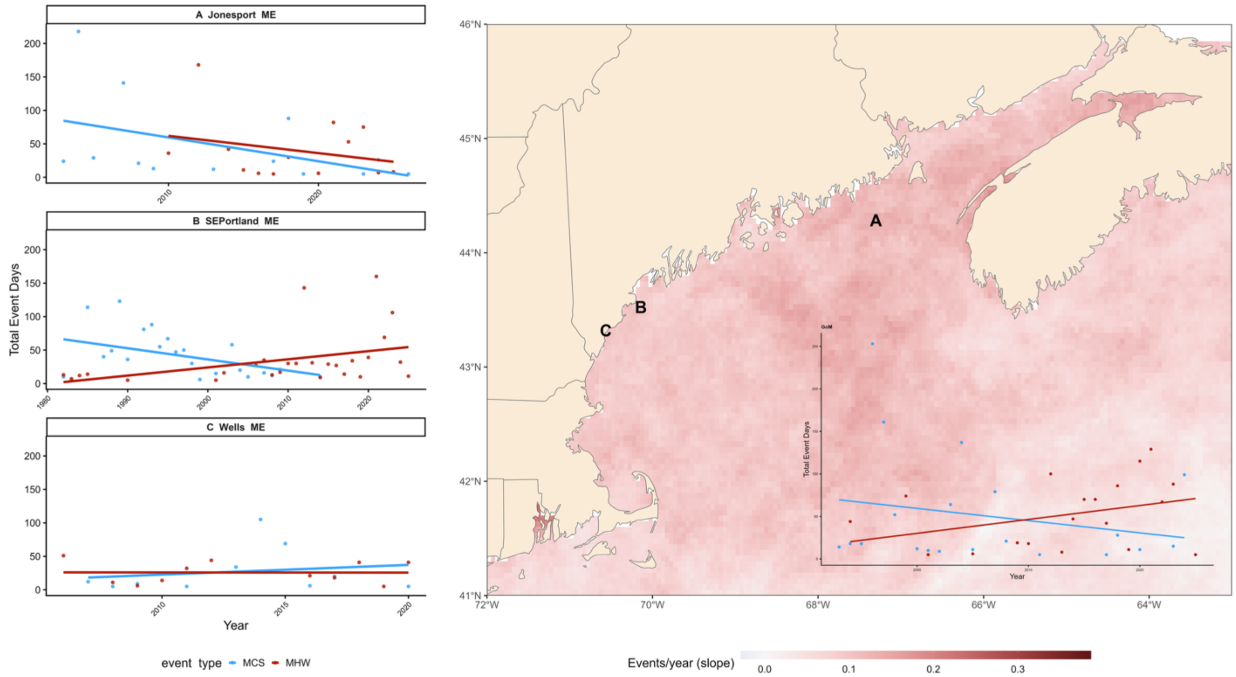


Figure 2. The left panel shows the number of extreme events per year, MHWs in red, and MCSs in blue for three representative buoys (see Appendix for all buoys analyzed). Headers show the corresponding buoy where data were collected. The right panel shows a map of the GoM, and darker colors represent an increased slope of MHWs for each pixel. The inset graph shows the number of MHW and MCS events per year in the whole GoM according to satellite-derived SST.

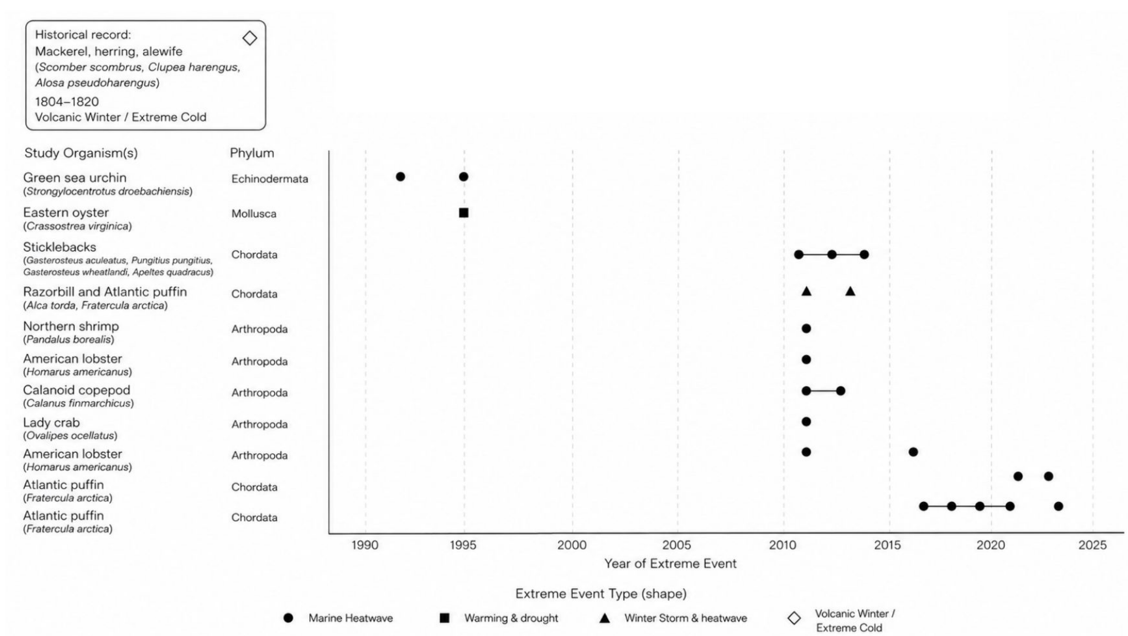


Figure 3. Timeline of extreme environmental events examined in marine organisms in the Gulf of Maine. Points represent individual event years, horizontal lines indicate consecutive event years, and symbols distinguish extreme event types. The 1804–1820 volcanic winter/extreme cold record falls outside the timeline and is shown separately in the inset box (see Table 1 for additional information).

Table 1. Summary of extreme events and impacts from our literature review.

Study Organism(s)	Location	Event Year	Extreme Event Type	Observed Impacts	Reference
Mollusca					
Eastern oysters (*Crassostrea virginica*)	Great Bay Estuary, New Hampshire/Maine, USA	1995	Warming & Drought	Disease Event, Population Decrease	(Barber et al., 1997)
Arthropoda					
Northern shrimp (*Pandalus borealis)*	Gulf of Maine†	2012	Marine Heatwave	Trophic Shift, Population Decrease	(Richards & Hunter, 2021)
American lobster (*Homarus americanus*)	Gulf of Maine†	2012	Marine Heatwave	Change in Human Activity	(K. Mills et al., 2017)
Lady crab (*Ovalipes ocellatus*)	Gulf of Maine†	2012	Marine Heatwave	Physiological Impacts	(Johnson et al., 2025)
Copepod (*Calanus finmarchicus*)	Southern Gulf of Maine †	2012-2013	Marine Heatwave	Physiological Impacts	(Runge et al., 2015)
American lobster (*Homarus americanus*)	Gulf of Maine†	2012, 2016	Marine Heatwave*	Change in Human Activity, Population Increase	(A. Pershing et al., 2018)
Echinodermata					
Green sea urchin (*Strongylocentrotus droebachiensis*)	Little Duck Island & Mill Cove, Nova Scotia, Canada	1993, 1995	Marine Heatwave	Disease Event, Population Decrease	(Scheibling & Hennigar, 1997)
Chordata					
Mackerel (*Scomber scombrus*), herring (*Atlantic herring*), alewives (*Alosa pseudoharengus*)	Gulf of Maine†	1804-1820	Volcanic Winter/Extreme Cold	Change in Human Activity, Population Decrease (Alewife), Population	(Alexander et al., 2017)

				Increase (Mackerel, Herring)	
Threespine stickleback (*Gasterosteus aculeatus*); ninespine stickleback (*Pungitius pungitius*); blackspotted stickleback (*Gasterosteus wheatlandi*); fourspine stickleback (*Apeltes quadracus*)	Cobscook Bay, Maine, USA	2011-2013	Marine Heatwave	Physiological Impacts, Population Increase	(McCleave et al., 2018)
Razorbills (*Alca torda*); Atlantic Puffins (*Fratercula arctica*)	Cape Cod, Massachusetts to Florida, USA	2012, 2013	Winter Storm & Heatwave	Trophic Shift, Population Decrease	(Diamond et al., 2020)
Atlantic Puffins (*Fratercula arctica*)	Seal Island National Wildlife Refuge, Maine, USA	2017-2020, 2022	Marine Heatwave*	Trophic Shift	(Wallace et al., 2025)
Atlantic puffin (*Fratercula arctica*)	Matinicus Rock, Maine, USA	2021, 2022	Marine Heatwave	Trophic Shift, Population Decrease	(Kennerley et al., 2024)

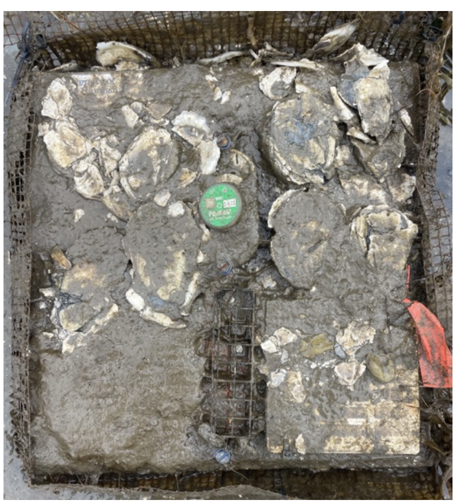
*Studies that used Hobday et al. (2016)'s definition of a heatwave, otherwise still described as anomalous, but another definition was used. See Table S3.

† Specific locations are listed where the study was site-based; broader regions are noted otherwise

Box 1. Intertidal ice scour review

Our literature review revealed a common subcategory of winter MCS impacts: ice scour. While selecting papers for our formal literature review, we opportunistically reviewed seven papers that discussed ice scour events across northern latitudes. Sea ice occurs along intertidal zones during winter and crushes, scrapes, and gouges habitats, increasing winter mortality (Gill et al., 2024). This results in the creation of alternative stable states and long-lasting changes to interspecies and trophic dynamics.

Ice scour events have diverse impacts on intertidal communities and habitats in the GoM. For example, Dudgeon & Petraitis, 2001 found that when ice scour scrapes intertidal zones and removes large clearings (4 to 8 m) of brown algae *Ascophyllum nodosum*, recruitment of mussels increases, which results in the creation of an alternative stable state dominated by mussel beds instead of macroalgal canopies (*Fucus vesiculosus* or *A. nodosum*). Switches in dominant species also dictate the type of predators present in the microhabitat, thus controlling abundance and recruitment of the dominant species (Dudgeon and Petraitis 2001). Ice scour can also indirectly cause mortality. For example, ice conditions in the Bay of Fundy resulted in significant *Corophium* amphipod mortality when rafting ice relocated them to uninhabitable areas (Wilson Jr., 1989). Beyond the community level, ice scour can produce positive ecosystem-level effects. Shallow macrophyte populations (e.g., *Ascophyllum nodosum)* that are redistributed and transported by ice scour pruning may provide significant nutrient sources and add to the nitrogen pool in estuaries (Mathieson et al., 1982).



In the past 380 years, sea ice occurred in about 86 winters in the GoM, with intertidal surfaces scraped clean about once every 25 years (Dudgeon and Petraitis 2001). These ice scour events have relocated species and nutrients, as well as created alternative stable states, which impact species interactions and ecosystems. As MCS duration declines in the GoM, ice scour events and their impacts will likely decline as well.

(left) Eastern oysters *Crassostrea virginica* crushed by sea ice in Great Bay, NH during winter 2026 (Cheng, 2026).

Supplementary material
Temperature extremes in the Gulf of Maine: A synthesis of marine heatwaves, cold-spells, and ecological impacts

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All data and code associated with this project is available at:

https://github.com/QuantMarineEcoLab/gulfmaine_extremeevents

Appendix S1 Long-term temperature extremes trends

We calculated daily mean averages for both the local (buoy) and the large-scale (satellite-derived sea surface temperatures) datasets. We evaluated changes in temperature trends by fitting linear models using the mean daily SST value as a response variable and years and a cyclic transformation of months as a seasonal predictor. We then grouped the number of days with extreme events per year and built linear models looking for signs of significant increases in extreme events. Annotated code used for all analysis can be accessed and branched from our GitHub Repository at https://github.com/QuantMarineEcoLab/gulfmaine_extremeevents

We screened our buoy datasets by the criteria presented in Schlegel et al. (2021). We excluded stations if they met one or more of the following criteria: less than 15 years of available temperature observations, greater than 25% missing daily temperature observations across the full study period, greater than 50% missing observations within any individual year, multi-year temporal gaps (>2 consecutive years missing), or consistent incomplete seasonal coverage during the primary marine heatwave season (April–November). Out of the 41 buoys in the GoM, 12 of them met the minimum requirements for analysis. Each buoy dataset was then manually screened and cleaned for erroneous data points that were not flagged in initial QA/QC.

Appendix S1.1 Additional temperature extremes data analysis

Figure S1: Trends in the annual frequency of extreme sea surface temperature (SST) events across the Gulf of Maine. On the left: Marine Heatwaves (MHWs) as number of days in a year above the 90th percentile value. On the right: Marine Cold-Spells (MCSs) as number of days below the 10th percentile. Points indicate the observed number of extreme days per year, grouped by percentile facets. Solid lines represent trendlines fitted using generalized linear models (GLMs) with a quasipoisson distribution and a log link function, which accounts for overdispersion in the count data. Shaded gray regions denote the 95% confidence intervals.

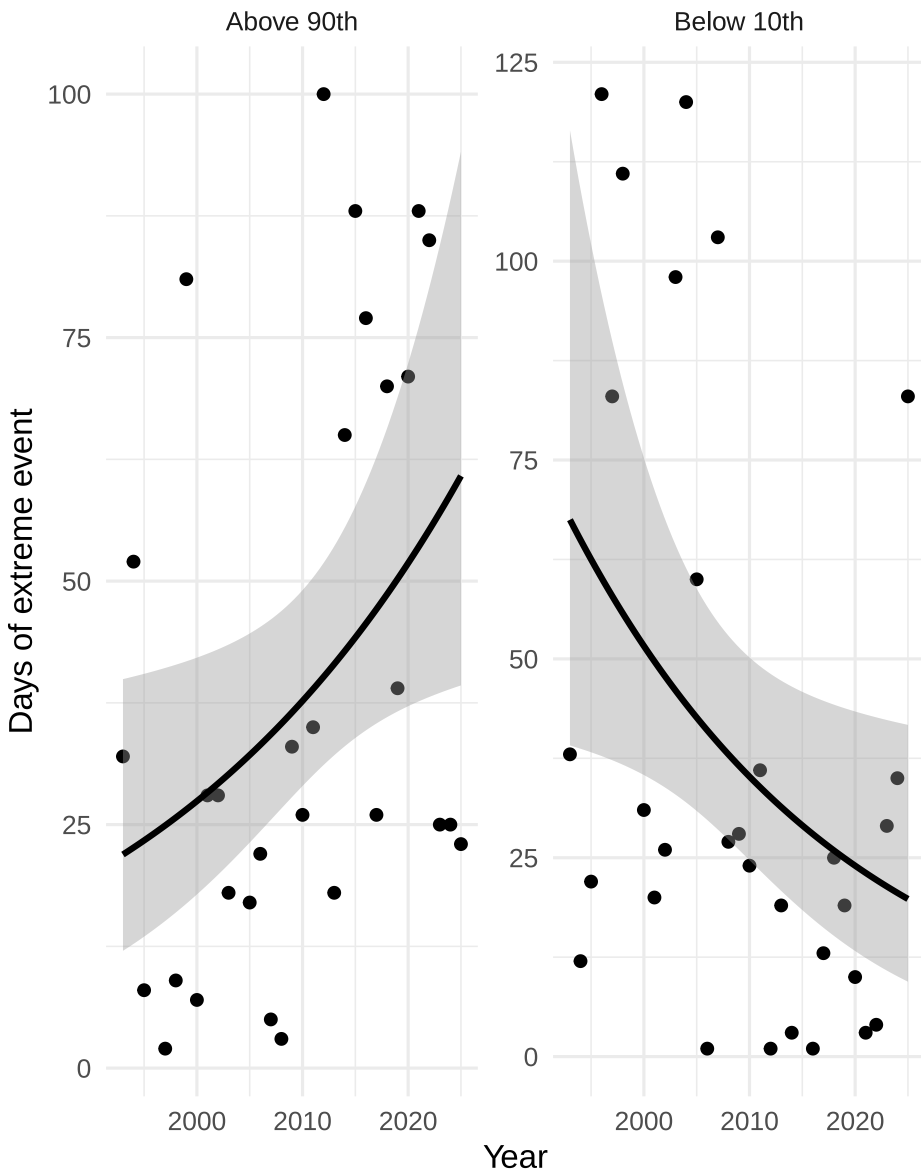


Table S1: Years with higher number of extreme event days. Location shows where the temperature data was collected. GoM data was collected from satellites, while other location data was collected from buoys."

Event	**Year**	**Location**	**Event Days**	**N Events**	**Max Intensity**
MCS	1987	GoMBuoy_ME	187	7	-1.1678
MCS	1987	NantucketOffshore_MA	150	8	-1.4887
MCS	1989	SEPortland_ME	123	4	-2.0259
MCS	1992	BostonBuoy_MA	157	9	-1.8590
MCS	1996	GoM	253	5	-1.5122
MCS	2004	Jonesport_ME	218	8	-1.4399
MCS	2007	Portland_ME	107	11	-1.6136
MCS	2008	JeffreysLedge_NH	165	6	-1.3660
MCS	2014	Wells_ME	105	5	-2.8540
MCS	2015	BarHarbor_ME	91	2	-2.2592
MCS	2015	BlockIsland_RI	76	2	-2.8770
MCS	2015	NantucketSound_MA	68	3	-2.0352
MCS	2017	CapeCodBay_MA	71	5	-2.2547
MCS	2019	CutlerWharf_ME	88	6	-0.8354
MHW	2006	Wells_ME	51	4	3.8900
MHW	2011	BarHarbor_ME	181	3	5.0296
MHW	2012	BlockIsland_RI	122	3	4.7313
MHW	2012	CutlerWharf_ME	111	6	1.7456
MHW	2012	GoMBuoy_ME	192	6	5.2133
MHW	2012	Jonesport_ME	168	9	4.7625
MHW	2012	Portland_ME	249	11	5.1014
MHW	2016	BostonBuoy_MA	191	7	3.9329

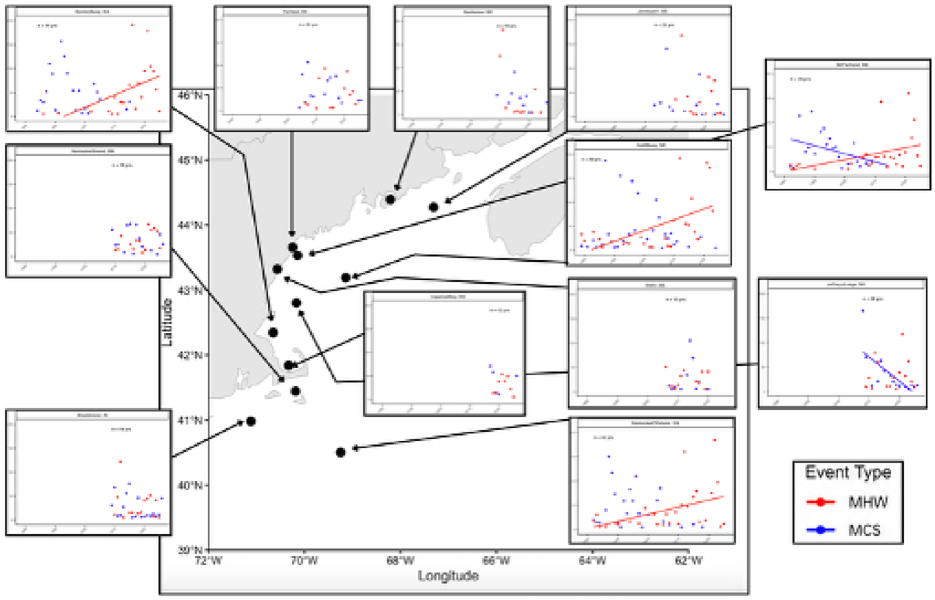
(continued)

Event	Year	Location	Event Days	N Events	Max Intensity
MHW	2021	GoM	129	6	2.2372
MHW	2021	CapeCodBay_MA	53	6	3.6034
MHW	2021	JeffreysLedge_NH	117	4	2.9302
MHW	2021	NantucketSound_MA	67	4	3.2362
MHW	2021	SEPortland_ME	160	5	4.4456
MHW	2022	NantucketOffshore_MA	184	7	5.9453

Table S2: Maximum intensity extreme events by site. Location shows where the temperature data was collected. GoM data was collected from satellites, while other location data was collected from buoys."

Event	Location	Year	Event Days	N Events	Max Intensity
MCS					
MCS	1987	GoMBuoy_ME	187	7	-1.1678
MCS	1987	NantucketOffshore_MA	150	8	-1.4887
MCS	1989	SEPortland_ME	123	4	-2.0259
MCS	1992	BostonBuoy_MA	157	9	-1.8590
MCS	1996	GoM	253	5	-1.5122
MCS	2004	Jonesport_ME	218	8	-1.4399
MCS	2007	Portland_ME	107	11	-1.6136
MCS	2008	JeffreysLedge_NH	165	6	-1.3660
MCS	2014	Wells_ME	105	5	-2.8540
MCS	2015	BarHarbor_ME	91	2	-2.2592
MCS	2015	BlockIsland_RI	76	2	-2.8770
MCS	2015	NantucketSound_MA	68	3	-2.0352
MCS	2017	CapeCodBay_MA	71	5	-2.2547
MCS	2019	CutlerWharf_ME	88	6	-0.8354
MHW					
MHW	2006	Wells_ME	51	4	3.8900
MHW	2011	BarHarbor_ME	181	3	5.0296
MHW	2012	BlockIsland_RI	122	3	4.7313
MHW	2012	CutlerWharf_ME	111	6	1.7456
MHW	2012	GoMBuoy_ME	192	6	5.2133
MHW	2012	Jonesport_ME	168	9	4.7625
MHW	2012	Portland_ME	249	11	5.1014
MHW	2016	BostonBuoy_MA	191	7	3.9329
MHW	2021	GoM	129	6	2.2372
MHW	2021	CapeCodBay_MA	53	6	3.6034
MHW	2021	JeffreysLedge_NH	117	4	2.9302
MHW	2021	NantucketSound_MA	67	4	3.2362
MHW	2021	SEPortland_ME	160	5	4.4456
MHW	2022	NantucketOffshore_MA	184	7	5.9453

Figure S2: Annual MHW and MCS days across selected buoys stations in the Gulf of Maine. Trend lines are shown only for significant linear relationships ($p < 0.05$). Values in the upper corners of each plot indicate the total number of years included in each buoy time series



Appendix S2 Literature Review

We performed a systematic mapping review, a technique involving a systematic search of the literature with the goal of mapping current research and identifying gaps in the field (Grant and Booth 2009).

Appendix S2.1 Systematic Search

We systematically searched the titles, abstracts, and keywords of articles in the Scopus database using iterative combinations of search terms designed to target studies of ecological impacts of extreme temperature events in the Gulf of Maine. After 18 iterations, we settled on a search strategy comprising 45 search terms, which returned 539 articles.

Appendix S2.2 Screening

We screened the 539 results using the following inclusion criteria:

1. Was the study area inside or overlapping the Gulf of Maine?
2. Did the paper analyze impacts from an extreme temperature event?
3. Was the study area a coastal, estuarine, or marine environment?
4. Did the study investigate ecological responses to an extreme temperature event?
5. Was the analysis performed on observational field data?

Articles for which the answer to any of these questions was “no” were excluded from the review.

We defined the **Gulf of Maine** as the marine and estuarine environments between Cape Cod and the southern coast of Nova Scotia. We defined **extreme temperature events** as periods of anomalously warm or cold water temperatures relative to contemporaneous conditions, lasting between one week and one season. We chose to exclusively review papers analyzing field observations in order to assess *in situ* impacts of extreme temperature events. Laboratory studies examining thermal tolerance and carryover effects, while valuable for producing nuanced hypotheses about historical impacts and forecasting future effects, were outside the scope of this review.

Of the 539 articles, 18 passed screening and were carried forward for full review.

Appendix S2.3 Full-Text Review

Each article that passed screening was read independently by two co-authors. Readers recorded:

- The specific location of the study
- The years the study was conducted and the dates of the relevant extreme temperature event
- Whether study authors mathematically identified the extreme temperature event and, if so, the identification technique employed
- The study organism(s) and the observed ecological effects of the extreme temperature event

Six articles were removed during this stage — either because the study area fell outside the Gulf of Maine, or because the paper addressed impacts from long-term temperature trends rather than seasonally discrete extreme events. This left **12 papers** in the final review.

Appendix S2.4 Search Terms

The following search terms were entered into the Scopus Documents Search to identify articles for the literature review. All searches were performed within article titles, abstracts, and keywords. The search was executed on **March 12, 2026** and returned **539 articles**.

(“Gulf of Maine” OR “Cape Cod” OR “WHOI” OR “GMRI” OR “Shoals Marine Lab” OR “Bigelow” OR “Darling Marine Center” OR “Center for Coastal Studies” OR “Plum Island*” OR ”Cape Ann*” OR “Isle of Shoals” OR “Bay of Fundy” OR Merrimack* OR “Hampton-Seabrook” OR Piscataqua* OR Saco* OR Casco* OR Androscoggin* OR Kennebec* OR Sheepscot* OR Damariscotta* OR Penobscot* OR Passamaquoddy* OR NERACOOS OR NERRS OR “National estuarine research reserve” OR “Great Bay Estuary” OR “Northwest Atlantic”)

AND

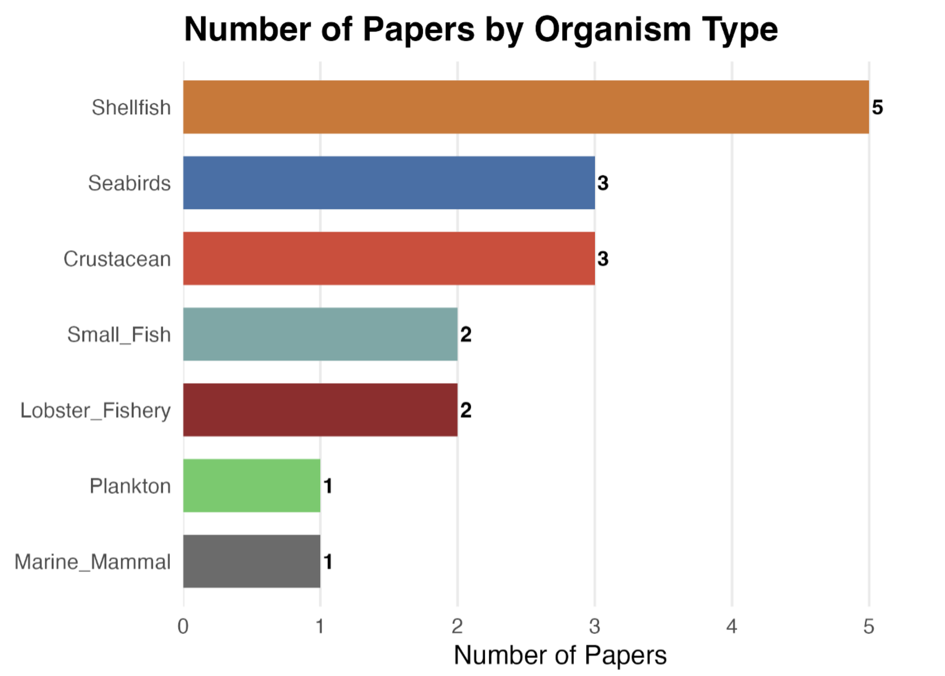
(“heatwave*” OR ”heat wave*” OR “unusual* warm*” OR ”abnormal* warm*” OR ”abnormal temperature*” OR “temperature event*” OR ”extreme event*” OR “heat event*” OR ”heat extreme*” OR “extreme warm*” OR ”extreme heat*” OR “extreme temperature*” OR ”coldspell*” OR “cold spell*” OR ”cold snap*” OR “extreme cold” OR “cold extreme*” OR ”coldwave*” OR “cold wave*” OR ”cold surge*” OR “freez*” OR “ice”)

AND NOT

(“ice age” OR “ice-age”)

Appendix S2.5 Additional literature review results

Figure S3: Number of papers by organism type



Appendix S2.6 Extra Information re: Extreme Event Types, from Table 1

Many studies that we found in our literature review made reference to Hobday et al. (2016) as a way to define the Extreme Event that was recorded in their study. Other studies used other definitions, these are included in the table below (Table S3).

Table S3: Full extreme event definitions from studies listed in Table 1 that did not use the Hobday et al. (2016) definition of a Marine Heatwave.

Reference	Extreme Event Type	Definition
Barber et al. 1997 The Journal of Parasitology	Warming & Drought	Unusually warm and dry climatic conditions that resulted in record-high water temperatures and salinities in the Great Bay Estuary, making it the warmest and driest year recorded for the region since 1949. They used a cumulative ranking score system to place the collected estuarine data into context with New Hampshire meteorological data that has a time series from 1895 to 1995. There are defined annual time periods that receive a score for their temperature and runoff. These values are added together to compare years for their drought index. Climatological data was obtained from 'the New Hampshire state meteorologist'.
Richards & Hunter 2021 Plos One	Marine Heatwave	Mean sea surface temperatures 2C above the 1982-2011 average all year and abnormally high bottom temperatures in summer and fall and 3-week early onset of spring conditions.

(continued)

Reference	Extreme Event Type	Definition
Mills et al. 2017 Frontiers in Marine Science	Marine Heatwave	"During 2012, sea surface temperatures on the northeast U. S. continental shelf were 1–3 ∘ C warmer than the 1982–2011 average, the highest documented in 150 years of measurements (Friedland, pers. comm.) and on par with the mean sea surface temperature change that climate models project for the region by the end of the century (Mills et al., 2013)."
Johnson et al. 2025 Journal of Crustacean Biology	Marine Heatwave	Monthly mean sea surface temperature in 2023 were 1.2C higher than the 2001-2024 mean at 1m and 1.4C higher at 50m (measured from a buoy in NERACOOS Bay). "Sea-surface temperature at 1 m in the Gulf of Maine was higher than the mean for every month but August 2023, and water temperature at 50 m was higher than the mean throughout the year. Maximum mean monthly temperature in 2023 peaked at 1 m in July at 19.8°C, and at 50 m in November at 10.9°C. For comparison, the Gulf of St. Lawrence is also warming but has later summer peaks in temperature (August) that are lower than the Gulf of Maine. Mean monthly sea surface temperature in 2021 peaked in the Gulf of St. Lawrence at approximately 18°C in August (Galbraith et al., 2022)."

(continued)

Reference	Extreme Event Type	Definition
Runge et al. 2015 Journal of Plankton Research	Marine Heatwave	"Warming Event" defined as surface water temperatures in spring and summer being 4-5C warmer than the seasonal average, underlying deep water warmer than average in late spring - late January (7-8C by June, 11-12C by late November).
Scheibling & Hennigar 1997 Marine Ecology Progress Series	Marine Heatwave	"Unusually warm sea surface temperature in late summer/fall (~3 degree C) Positive deviation (anomaly) from long-term average mean monthly temp (1926-1967) (Miller & Colodey 1983, Scheibling & Stephenson 1984, Miller 1985, Scheibling 1986)"
Alexander et al. 2017 Science Advances	Volcanic Winter/Extreme Cold	Indonesian volcano Tambora exploded, resulting in 100 cubic km of ash, increased sulfate aerosols, decreased global temperatures by 1-1.5C, unseasonable cold + droughts/floods. Daily average temperatures (from historical reconstruction, from Salem, MA) were more than 1 standard deviation lower than adjacent years. Temperature differential was 1 standard deviation higher than adjacent years.
McCleave et al. 2018 Environmental Biology of Fishes	Marine Heatwave	No specific event deduction conduced, simply relayed the details of the known 2012 Marine Heatwave event in the Gulf of Maine; e.g. reported the 1-4C anomaly observed in the Central Gulf of Maine by a National Data Buoy Center buoy.

(continued)

Reference	Extreme Event Type	Definition
Diamond et al. 2020 Marine Ornithology	Winter Storm & Heatwave	A "strong ECWS" (East Coast Winter Storm) is defined by a higher wind threshold (at least 45 kt [83 km/h] for at least 12 h). Heatwave definition: Temperatures 1 to 3 degrees Celsius above mean, 3.5 standard deviations, or 'anomalously high sea surface temperature'.
Kennerley et al. 2024 Frontiers in Marine Science	Marine Heatwave	Marine Heatwave defined as something that "temporarily – but often rapidly – bring anomalously warm conditions to a region, altering the distribution of thermal habitat (Lonhart et al. 2019; Jacox et al. 2020)."

Galbraith et al. (2022), Jacox et al. (2020), Lonhart et al. (2019), Miller and Colodey (1983), Miller (1985), Mills et al. (2013), R. E. Scheibling and Stephenson (1984), R. Scheibling (1986)

References

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Lonhart, Steve I., Rikke Jeppesen, Rodrigo Beas-Luna, Jeffrey A. Crooks, and Julio Lorda. 2019. "Shifts in the Distribution and Abundance of Coastal Marine Species Along the Eastern Pacific Ocean During Marine Heatwaves from 2013 to 2018." *Marine Biodiversity Records* 12 (1): 13. https://doi.org/10.1186/s41200-019-0171-8.

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Mills, Katherine E., Andrew J. Pershing, Curtis J. Brown, Yong Chen, Fu-Sung Chiang, Daniel S. Holland, Sigrid Lehuta, et al. 2013. "Fisheries Management in a Changing Climate: Lessons from the 2012 Ocean Heat Wave in the Northwest Atlantic." *Oceanography* 26 (2): 191–95. https://www.jstor.org/stable/24862052.

Scheibling, R. E., and R. L. Stephenson. 1984. "Mass Mortality of Strongylocentrotus Droebachiensis (Echinodermata: Echinoidea) Off Nova Scotia, Canada." *Marine Biology* 78 (2): 153–64. https://doi.org/10.1007/BF00394695.

Scheibling, Robert. 1986. "Increased Macroalgal Abundance Following Mass Mortalities of Sea Urchins (Strongylocentrotus Droebachiensis) Along the Atlantic Coast of Nova Scotia." *Oecologia* 68 (2): 186–98. https://doi.org/10.1007/BF00384786.

Schlegel, Robert W., Sofia Darmaraki, Jessica A. Benthuysen, Karen Filbee-Dexter, and Eric C. J. Oliver. 2021. "Marine Cold-Spells." *Progress in Oceanography* 198 (November): 102684. https://doi.org/10.1016/j.pocean.2021.102684.