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REVIEW

Climate impacts on the Gulf of Maine ecosystem: A review of observed and expected changes in 2050 from rising temperatures

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The Gulf of Maine has recently experienced its warmest 5-year period (2015–2020) in the instrumental record. This warming was associated with a decline in the signature subarctic zooplankton species, *Calanus finmarchicus*. The temperature changes have also led to impacts on commercial species such as Atlantic cod (*Gadus morhua*) and American lobster (*Homarus americanus*) and protected species including Atlantic puffins (*Fratercula arctica*) and northern right whales (*Eubalaena glacialis*). The recent period also saw a decline in Atlantic herring (*Clupea harengus*) recruitment and an increase in novel harmful algal species, although these have not been attributed to the recent warming. Here, we use an ensemble of numerical ocean models to characterize expected ocean conditions in the middle of this century. Under the high CO_2 emissions scenario (RCP8.5), the average temperature in the Gulf of Maine is expected to increase 1.1°C to 2.4°C relative to the 1976–2005 average. Surface salinity is expected to decrease, leading to enhanced water column stratification. These physical changes are likely to lead to additional declines in subarctic species including *C. finmarchicus*, American lobster, and Atlantic cod and an increase in temperate species. The ecosystem changes have already impacted human communities through altered delivery of ecosystem services derived from the marine environment. Continued warming is expected to lead to a loss of heritage, changes in culture, and the necessity for adaptation.

Keywords: Gulf of Maine, Climate change, *Calanus*, Lobster, Squid, Right whale

Introduction

The ecosystems in the Gulf of Maine have provided food, recreation, and economic opportunities for centuries. Recently, the Gulf of Maine has experienced one of the fastest rates of warming of any ocean ecosystem (Pershing et al., 2015). Global climate projections suggest that this region will continue to warm at an above average rate (Saba et al., 2016). The recent warming has elevated concerns within the region about how marine resources and communities around the Gulf of Maine will fare as global warming progresses. These concerns prompted the creation of the Gulf of Maine 2050 International Symposium (from which emerged this special collection of papers).

As part of this symposium, we were asked to synthesize current understanding of how changes in ocean temperature have impacted ecosystems in the Gulf of Maine and how these ecosystems are likely to change by 2050. We relied on an ensemble of high-resolution projections for ocean conditions in our region (Brickman et al., 2021). This article complements other Gulf of Maine 2050

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scenario papers on ocean acidification (Siedlecki et al., 2021) and sea level rise and storms (Chisholm et al., 2021).

The year 2050 was not selected at random. Around this time, the different carbon emission scenarios begin to diverge from one another. In other words, many of the changes we expect over the next 30 years are inevitable, regardless of how much carbon dioxide is emitted in the next few years. By focusing on 2050, we anticipate the regional community can identify tangible goals that inform actions to help human and ecological systems adapt over the next few decades.

Because the signal of warming has been so strong, this article begins by reviewing what we have learned by studying ecosystem impacts from recent changes in temperature. We then summarize two independent efforts to develop high-resolution projections for conditions in 2050. Finally, we consider what the future changes may mean for the Gulf of Maine marine ecosystem. We also present four case studies that offer an integrated perspective on the future of some highly visible and commercially important species.

Observed impacts of warming on the Gulf of Maine ecosystem

The Newfoundland/Labrador Shelf, Gulf of St. Lawrence, Scotian Shelf, and Gulf of Maine form an interconnected shelf sea along the eastern seaboard of the United States and Canada. The circulation in the region is characterized by a general northeast–southwest flow of water from the Labrador and Newfoundland Shelf areas through the Gulf of St. Lawrence, Scotian Shelf, and Gulf of Maine to the Mid-Atlantic Bight (**Figure 1**). The region off the shelf is the confluence zone between the warm northeastward flowing Gulf Stream and the cold southwestward flowing Labrador Current (Loder et al., 1998). Whether the water in this region has temperate or subpolar characteristics depends on conditions in the broader North Atlantic. Notably, weaker Atlantic meridional overturning circulation is associated with warmer conditions off the continental shelf and warmer water entering the Gulf of Maine through the Northeast Channel (Saba et al., 2016; Caesar et al., 2018; Record et al., 2019b). Ocean properties in the Gulf of Maine are also directly influenced by Gulf Stream variability (i.e., warm-core rings), inflows of water from the Scotian Shelf, and local effects like river inputs and interaction with the atmosphere.

Due to the input of cold water from the Scotian Shelf, the Gulf of Maine has a distinctive subarctic ecosystem despite having a mean latitude of 41°N. It has a strong spring phytoplankton bloom typical of the North Atlantic that is fueled by nitrate that mixes into the surface waters by the cold winters or, in places like Georges Bank, by the strong tides (Townsend, 1991). The copepod *Calanus finmarchicus* (hereafter, *Calanus*) is the signature invertebrate animal of the North Atlantic subpolar ecosystem (Pershing and Stamieszkin, 2020). It is adapted to the intense seasonality of this region. In particular, it accumulates reserves of lipids during the spring and summer and then uses these reserves to sustain itself through several months of winter dormancy (Johnson et al., 2007).

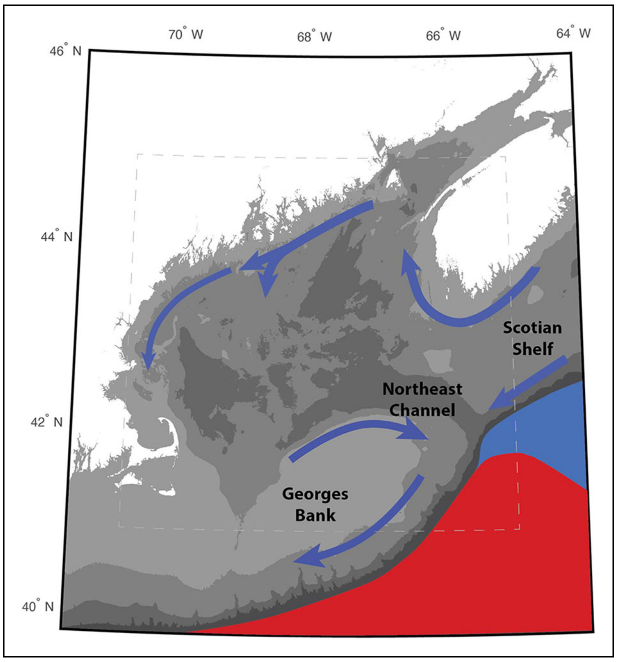

Figure 1. Map of the Gulf of Maine with major currents highlighted. The red and blue areas off the continental shelf represent the cold and warm water masses, respectively, that can enter the Gulf of Maine at depth (see MERCINA Working Group, 2001). As in Pershing et al. (2015), temperature observations from NOAA extended reconstruction sea surface temperature data (see Data accessibility statement) were averaged over the region encompassed by the dashed line. Downscaled climate model output was averaged over the entire shelf area in the image. DOI: https://doi.org/10.1525/elementa.2020.00076.f1

Calanus is very abundant in the Gulf of Maine—some of the highest concentrations ever measured are from this region, even though the Gulf is near the southern limit of its range (Melle et al., 2014; Pershing and Stamieszkin, 2020).

The spring bloom and *Calanus* support a community of iconic North Atlantic species, with a large proportion of the carbon fixed during the spring bloom likely passing to higher trophic levels through *Calanus* (Pershing and Stamieszkin, 2020). *Calanus* is an important food source for larval Atlantic cod (*Gadus morhua*), adult Atlantic herring (*Clupea harengus*), sand lance (*Ammodytes* spp.), and right whales (*Eubalaena glacialis*). Small fish like herring and sand lance are key seasonal prey for larger fish like adult cod and bluefin tuna (*Thunnus thynnus*) and for marine mammals and seabirds (Golet et al., 2015; Smith et al., 2015; Staudinger et al., 2020).

Temperature in the Gulf of Maine varies from year to year and from decade to decade (**Figure 2**). Mean surface temperatures in the late 1940s and early 1950s were well above the 1976–2005 mean, and 1949 and 1951 had annual anomalies above 1°C. (Note: all physical changes in this article are reported relative to the 1976–2005 climatology, which provides a consistent 30-year reference period that works for both the observations and climate

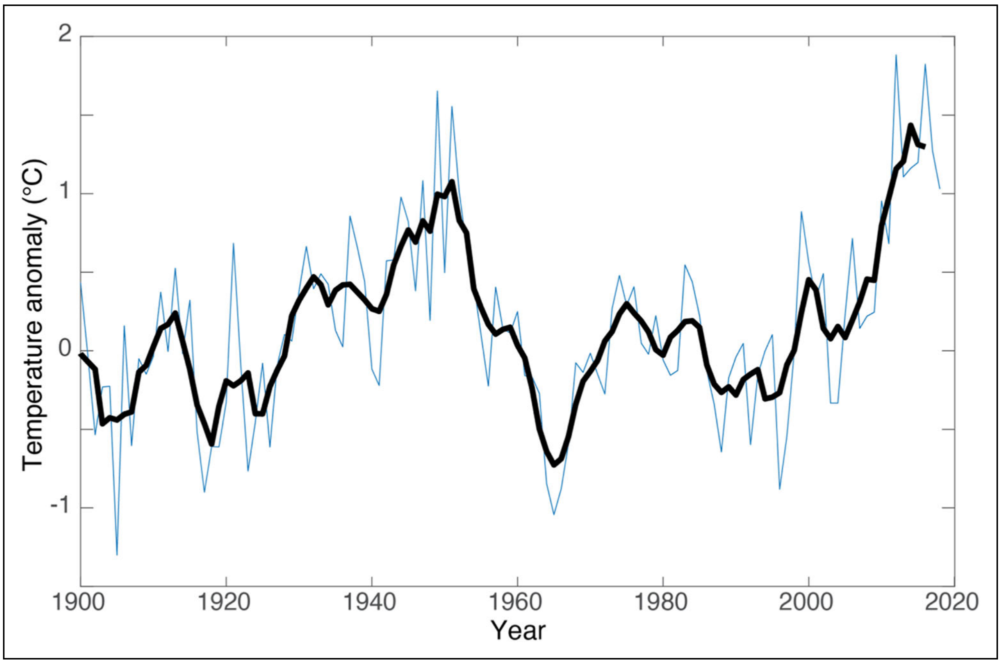

Figure 2. Gulf of Maine temperature anomalies relative to 1976–2005 baseline. Thin line indicates annual average temperature; thick line, 5-year running mean. Data from NOAA extended reconstruction sea surface temperature (see Data accessibility statement). DOI: https://doi.org/10.1525/elementa.2020.00076.f2

simulations). The 1960s were particularly cold. Temperatures rose in 1999 and then entered a period of rapid warming around 2005. The warming has been strongest in the summer and fall, with summer-like conditions starting about a month sooner and ending a month later than the historical record (Thomas et al., 2017). The warming was punctuated by heat waves in 2012 (Mills et al., 2013), 2016 (Pershing et al., 2018b), and 2018. The mean temperature over the last 5 years is now the highest on record. The recent warming has been linked to inflows of warm, salty water at depth through the Northeast Channel beginning in 2010 (Townsend et al., 2015; Brickman et al., 2018; Record et al., 2019b). This subsurface oceanographic pathway is highly sensitive to changes in the Atlantic meridional overturning circulation (Sherwood et al., 2011), which has been weakening due to Arctic warming (Caesar et al., 2018).

In addition, warmer winters with more precipitation falling as rain rather than snow have affected ice pack conditions in the watersheds of the Gulf of Maine and shifted the timing and amount of freshwater runoff and delivery to coastal waters (Hodgkins et al., 2003; Huntington and Billmire, 2014). As a result, seasonal stratification has become more variable, with a general trend toward earlier strengthening in the eastern portion of the Gulf of Maine basin (Li et al., 2015).

The recent warming is causing the Gulf of Maine ecosystem to lose some of its subarctic characteristics. *Calanus* abundance, especially in the eastern Gulf of Maine, has declined during the summer and autumn, and other small crustaceans including important prey species like euphausiids have also shifted northward (Lasley-Rasher et al., 2015). Stocks near the southern limit of their range such as northern shrimp (*Pandalus borealis*; Richards, 2012; Richards et al., 2012; Richards et al., 2016), Atlantic cod (Pershing et al., 2015), and southern New England American lobster (*Homarus americanus*; Le Bris et al., 2018) have declined (see Case study: Lobsters). Recent Atlantic herring recruitment has also been very low (Northeast Fisheries Science Center, 2018). While the decline in herring recruitment has not been attributed to temperature or to the changes in *Calanus*, it is certainly consistent with the general decline in the subarctic community. Many Northeast U.S. fishery stocks are moving northward and to deeper depths with long-term temperature changes across the region (Nye et al., 2009; Pinsky et al., 2013; Kleisner et al., 2016). In addition, warming-related declines in *Calanus* are causing right whales to spend more time in the Gulf of St. Lawrence, instead of in the Gulf of Maine (Record et al., 2019b; see Case study: Right whales).

Counter to declines in subarctic species is the increased prominence of mid-Atlantic species in the Gulf of Maine and the adjacent Scotian Shelf. Longfin squid (*Doryteuthis pealeii*), which are typically ephemeral off Maine, moved into and stayed in coastal Maine waters during the 2012 marine heat wave (Mills et al., 2013; see Case study: Squid). Black sea bass (*Centropristis striata*) have extended their range from Cape Cod Bay into the northern Gulf of Maine (McBride et al., 2018; McMahan and Grabowski, 2019) as have Atlantic mackerel (*Scomber scombrus*; Overholtz et al., 2011) and silver hake (*Merluccius bilinearis*; Nye et al., 2011). American lobster, which prefers relatively warmer temperatures, is rapidly increasing across the Scotian Shelf and expanding its distribution to the Eastern Scotian Shelf and into deeper water (Bernier et al., 2018). Some new species, like American John Dory (*Zeus faber*) and armored sea robin (*Peristedion miniatum*), are now observed more frequently on the Scotian Shelf (Bernier et al., 2018). Shifts in the Gulf of Maine fish community from subarctic to temperate composition and dominance are impacting the diet and breeding success of seabird species such as puffins and terns that nest during the summer months on coastal islands in the Gulf of Maine (Kress et al., 2016; see Case study: Seabirds).

In addition to distribution shifts in fishery-relevant species, warming waters are affecting a variety of other species in the Gulf of Maine. While green crabs (*Carcinus maenas*) have been present in the Gulf of Maine for more than 100 years, their abundance increased dramatically during the warm period in the 1950s (Glude, 1955; Welch, 1969). During recent warming, green crabs have caused considerable damage to eelgrass beds and to populations of soft-shell clams (*Mya arenaria*; Congleton 2006; Whitlow 2010; Belknap and Wilson, 2015; Neckles, 2015). They are one possible explanation for the observed decline in blue mussels (*Mytilus edulis*) throughout the Gulf of Maine (Sorte et al., 2017) and have the potential to impact native rock crabs (Griffen and Riley, 2015). Other non-native species, such as the tunicate, *Botrylloides violaceus*, have proliferated in the Gulf of Maine, altering communities that occupy rocky bottoms and settling on piers, fishing gear, and even seaweeds (Dijkstra et al., 2007).

Diseases that affect local species are also increasing in prevalence. An increase in the incidence of epizootic shell disease is part of the explanation for the decline in American lobster in southern New England after 1999 (Wahle et al., 2009). Oyster pathogens such as *Haplosporidium nelsoni* and *Perkinsus marinus* that, respectively, cause the diseases "MSX" (Multinucleated Sphere Unknown) and "Dermo" have become more prevalent in the Gulf of Maine as ocean temperatures have warmed (Marquis et al., 2015; Robledo et al., 2018). While there is no evidence to date that harmful algal blooms are increasing in the Gulf of Maine, blooms of species previously unreported in the Gulf of Maine like *Karenia mikimotoi* and *Pseudo-nitzschia australis* have occurred in the last several years (Clark et al., 2019; Record et al., 2021). Outbreaks of these organisms have been linked to fish and wildlife mortality events in other regions (e.g., Pacific coast) and represent an emerging threat if changing conditions in the Gulf of Maine support them (de la Riva et al., 2009; Record et al., 2021).

The distribution shifts reported above can occur through a variety of mechanisms. Highly mobile species like squid, butterfish (*Peprilus triacanthus*), and northern right whales can shift rapidly by actively tracking the environmental conditions they need to survive. For less mobile species and for plankton, shifts occur through spatial gradients in productivity and survival. For example, Le Bris et al. (2018) attributed the decline of the lobster population in southern New England and the increase in abundance in the northern Gulf of Maine to temperature-dependent recruitment.

Shifts are also occurring in the timing of when species are abundant or when processes like phytoplankton blooms occur. Seasonal changes in the environment, such as the timing of transition from winter to spring and fall to winter, are lengthening the duration of summer and shortening the duration of winter (Thomas et al., 2017). The fact that summer and fall temperatures have risen faster than those in the winter implies the likelihood of rapid drops in temperature during the late fall and early winter. This pattern may explain the recent increase in cold-stun stranding events of Kemp's Ridley sea turtles (*Lepidochelys kempii*; Pershing et al., 2018a; Griffin et al., 2019).

All of these physical changes in the seasonal conditions of the Gulf of Maine affect the timing of recurring life events, known as phenology, of marine fauna, including foraging and growth conditions, and environmental cues that prompt breeding and migration (Staudinger et al., 2019). The greatest evidence for phenological shifts in the Gulf of Maine have been observed at the base of the food web including later spring and fall phytoplankton blooms (Record et al., 2019a) and earlier and higher peaks in spring abundance of *Calanus* and other zooplankton (Runge et al., 2015; Record et al., 2019b). The phenological responses of larval fish abundance have varied widely across species, with earlier occurrence of larval stages of some benthic fishes (e.g., haddock—*Melanogrammus aeglefinus*, winter flounder—*Pseudopleuronectes americanus*) and later occurrence of species such as sand lance, pollock (*Pollachius virens*), and mackerel; however, most larval fish (e.g., Atlantic cod, silver hake) have shown no detectable changes (Walsh et al., 2015).

Evidence for shifts in phenology of higher trophic level species is scarce (Staudinger et al., 2019). A few notable examples include later reproduction and fledging of Atlantic puffins on Machias Seal Island (Whidden, 2016) and increased duration of the spawning period for some commercially important macro-invertebrates including northern shrimp (Richards, 2012; Richards et al., 2016). The arrival and departure of fin and humpback whales have shifted 11–28 days earlier in the Gulf of St. Lawrence (Ramp et al., 2015). In the Gulf of Maine, despite evidence for right whale distribution shifts (Davis et al., 2017; Record et al., 2019b), information on how the timing of habitat use may have changed is lacking. Charif et al. (2020) found suggestive correlations between winter sea surface temperature and the timing of whale presence in Massachusetts Bay, and they suggest that the right whales may be using that habitat earlier than in previous years. Additional analyses with long-term monitoring data are needed to understand phenological shifts in large whale habitat use in the Gulf of Maine. Nonuniform changes in phenology of marine animals put species at risk for ecological mismatches that can affect fitness and survival and have important consequences for interactions with human activities (Staudinger et al., 2019).

Ensemble projections for 2050

To assess how the ecosystems in the Gulf of Maine might change by 2050, we used the temperature projections from Brickman et al. (2021). These projections synthesize independent modeling efforts by Canadian and U.S. research groups. Both efforts used a common dynamical downscaling approach: force a high-resolution regional ocean model with output from global climate models.

Table 1. Assessment of expected changes in surface and bottom (50-m) conditions in the Gulf of Maine based on projections by Brickman et al. (2021). DOI: https://doi.org/10.1525/elementa.2020.00076.t1

Variable	Expectation[a]	Models
Surface temperature	Highly likely to increase	4/4
Surface salinity	Likely to decrease	3/4[b]
Bottom temperature	Highly likely to increase	4/4
Bottom salinity	Likely to increase	4/4
Stratification	Highly likely to increase	4/4

[a]Direction of change and likelihood was estimated based on number of models exhibiting that change.

[b]All models showed increases in some portion of the domain, but the considerable spatial variability led to reduced likelihood.

They differ in the ocean model used and in how they dealt with the ensemble of climate projections and the different climate scenarios.

The U.S. study used the Regional Ocean Modeling System. They conducted three independent runs forced by the output from one of three global models: GFDL ESM2M, Institut Pierre Simon Laplace CM5A-MR, and the Hadley Center HadGEM2-CC (HadGEM; see Alexander et al., 2020). Their study only considered the high emissions scenario (RCP8.5; Taylor et al., 2012).

The Canadian study used the Bedford Institute of Oceanography North Atlantic Model (BNAM). They used the ensemble average forcing from six earth system models from the CMIP5 ensemble (see Brickman et al., 2016). They considered the high emissions scenario and a moderate emissions scenario (RCP4.5) that has CO_2 concentrations stabilizing later in the century (Taylor et al., 2012).

The Brickman et al. (2021) projections suggest that the Gulf of Maine in 2050 will be warmer at both the surface and bottom under business-as-usual conditions (**Table 1**). It is likely to be fresher at the surface but saltier at depth, though there is more spatial variability in the bottom salinity. These features mean that the Gulf of Maine will be more stratified in the future. The rates of change for most processes are generally in line with recent observations. For example, two projections with the weakest surface warming had warming rates of 1.8°C and 2.7°C century^{-1}. These are well above the observed long-term (1900–2013) trend (0.6°C century^{-1}; Fernandez et al., 2015) but below the recent 30-year rate (3°C century^{-1} for 1982–2013; Pershing et al., 2015). The two warmest projections had rates of 3.2 and 3.8°C century^{-1}, comparable to the recent 30-year rate.

To provide some context for interpreting ecosystem change, we can benchmark the Brickman et al. (2021) projections against recent conditions. The ensemble average of the four RCP8.5 projections is 1.73°C above the 1976–2005 reference and slightly below conditions in 2012 (1.86°C) and 2016 (1.82°C; **Figure 3**). However, the Brickman et al. projections are best thought of as the 30-year mean at the middle of the century, which means that in 2050, the Gulf of Maine is likely to produce temperatures warmer than what we have experienced so far.

There is considerable variability in the four RCP8.5 simulations. The warmest simulation (HadGEM) has conditions in 2050 that are hard to fathom based on the recent history of the Gulf of Maine. The mean temperature anomaly in the HadGEM simulation is 2.38°C above the baseline. In the climate depicted in this simulation, the extreme (by current standards) conditions in 2012 would be a cool year. In contrast, the coolest simulation (BNAM) has temperatures in 2050 at 1.11°C above the 1976–2005 reference (**Figure 3**), which suggests a climate where an average year is similar to the current conditions and where conditions like those during the 2012 or 2016 heat waves would be merely warm years. The mean in this simulation is only 0.3°C warmer than the BNAM RCP4.5 simulation, underscoring the rationale for choosing 2050.

Ecosystem conditions in 2050

Quantitative models relating temperature to distribution and/or abundance are available for several important Gulf of Maine species. Climate model projections of temperature can then be used to drive these models, providing an estimate of the future abundance or distribution. For other important species, we can make inferences about how they have changed in response to past warming or cooling or how they are distributed along thermal gradients in space.

Projected impacts on Calanus

For *Calanus*, projections into future climate conditions have generally relied so far on statistical models. Using a model built on surface conditions, Reygondeau and Beaugrand (2011) predicted a disappearance of *Calanus* from the Gulf of Maine by 2050. Grieve et al. (2017) included bottom conditions—important because of the extended diapause period at depth—and predicted a more modest decline of around 50% by the end of the century. As yet, statistical models do not incorporate two key processes relevant to plankton: advection, which strongly influences *Calanus* abundance along coasts and continental shelves (Speirs et al 2006; Ji et al., 2017), and life history dynamics, for which a number of mechanistic models exist (reviewed by Record et al., 2013) but have not been used in projections. Wilson et al. (2016) did project one mechanistic *Calanus* model to end-of-century conditions and reported some of the largest decreases in diapause duration (approximately 75%) to occur in the Gulf of Maine, but what impact this decreased duration will have on overall abundance is not clear. Using a life-history model of *Calanus*, Ross et al. (2021) suggest a decline in the Gulf of Maine, especially in the summer and fall. Models used to date have not attempted to capture the capacity of *Calanus* to adjust behavior to changing conditions (Beever et al., 2016) or interactions among *Calanus* and other species within the food web, which could have either positive or negative effects (Moritz and Agudo, 2013; Selden et al., 2018). Also needed are improved models that better capture this species' interactions with the

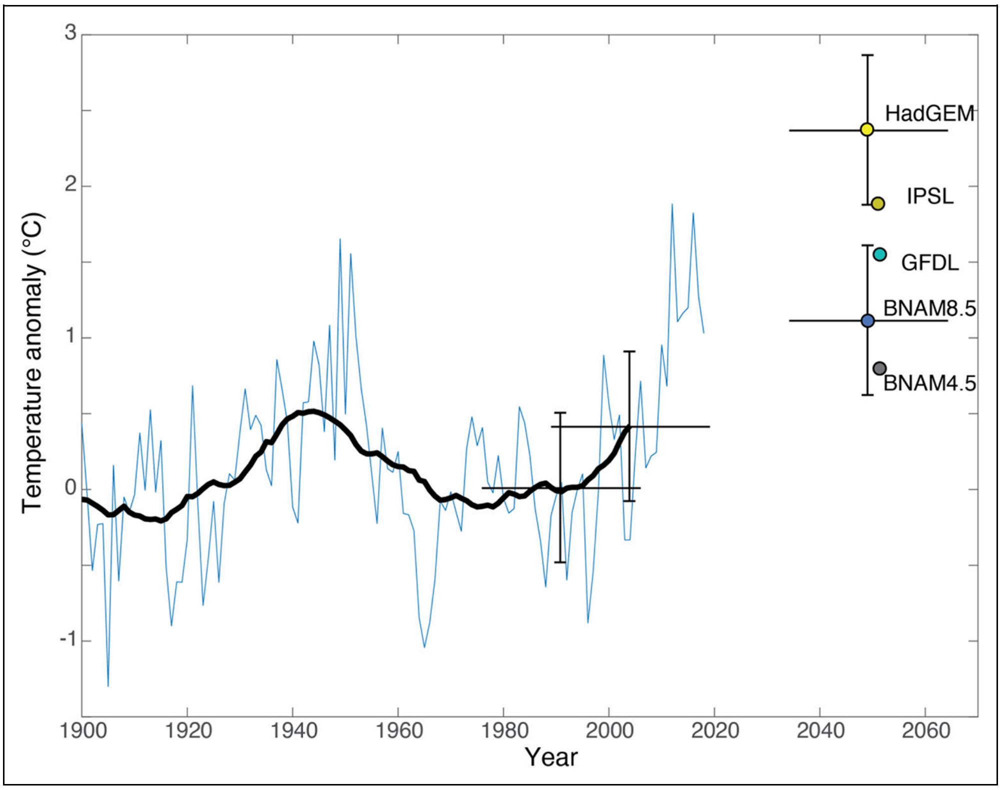

Figure 3. Observed and projected Gulf of Maine sea surface temperature anomalies relative to 1976–2005 baseline. Thin line indicates annual average temperature (as in **Figure 2**); thick line indicates 29-year running mean. The colored circles denote the mean projections from the five downscaled climate projections. The projections represent the 30-year climate centered on 2050. The crosses denote the 30-year period represented by the reference period, the most recent observations, and the RCP8.5 projections with the least and most warming. The vertical extent of the crosses shows variability of ± 0.5°C consistent with the observations. The gray circle is the mean from the Bedford Institute of Oceanography North Atlantic Model RCP4.5 projection. DOI: https://doi.org/10.1525/elementa.2020.00076.f3

circulation and patterns of primary productivity that may allow the Gulf of Maine to function as a refugia for *Calanus* (Runge et al., 2015).

Projected impacts on fish species

In the Gulf of Maine, continued warming is expected to create extensive changes in finfish and shellfish by 2050. Overfished stocks near the upper thermal limit of their range are most likely to experience distribution and abundance change and thus will be vulnerable to further impacts. Hare et al. (2016) conducted a climate vulnerability assessment for 82 fish and invertebrate species on the Northeast U.S. Shelf. Their methods indicated that the overall climate vulnerability is high to very high for half the species assessed, with bivalves (i.e., bay scallop—*Argopecten irradians*, ocean quahog—*Arctica islandica*, northern quahog—*Mercenaria mercenaria*) and an endangered fish (i.e., Atlantic salmon—*Salmo salar*) rated the most vulnerable. In addition, the majority of species have a high potential for changes in distribution in response to projected changes in climate. Negative effects are expected for half of the species assessed, and many of those species are currently important to commercial fisheries in the Gulf of Maine. Some species that have been observed moving into the Gulf of Maine, such as black sea bass and longfin squid, are expected to be affected positively (e.g., increase in productivity and abundance) over the Northeast Shelf region. A similar vulnerability assessment of marine species on the Scotian Shelf predicts that 45% of populations may be vulnerable under a severe (+3°C) warming scenario (Stortini et al., 2015). Key commercial populations on the western Scotian Shelf (adjacent to the Gulf of Maine) that are vulnerable under the severe warming scenario include snow crab (*Chionoecetes opilio*), cod, pollock, and red hake (*Urophycis chuss*).

Projected warming also affects thermal habitats for species occurring in the Gulf of Maine, and three studies have provided species distribution projections for the Gulf of Maine and the surrounding region. Allyn et al. (2020) used CMIP5 projections for 2050 that are in the middle range of the Brickman et al. (2021) projections. Kleisner et al. (2017) and Shackell et al. (2014) used temperature projections that are higher than the Brickman et al. projections. Despite their differences, all three studies indicate that by 2050, the Gulf of Maine will experience declines in thermal habitat area and biomass of key species that are currently familiar in the region, including many species of groundfish (e.g., Atlantic cod, haddock, Acadian redfish—*Sebastes fasciatus*), Atlantic herring, and red crab (*Chaceon quinquedens*). They also project gains in more southern species (e.g., summer flounder—*Paralichthys dentatus*, striped bass—*Morone saxatilis*, bluefish—*Pomatomus saltatrix*, smooth dogfish—*Squalus acanthias*). As these southern species move northward in response to rising ocean temperatures, they are expected to become more prevalent in the Gulf of Maine by 2050 (Allyn et al., 2020).

Projections tailored to individual species indicate more nuanced ways in which warming may affect suitable habitats and species distributions. Fragmentation of habitats is one concern. For an increase of 1°C in bottom temperature (the low end of the Brickman et al. projections), cusk (*Brosme brosme*) habitat in the Gulf of Maine region will shrink and fragment as a result of a spatial mismatch between high complexity seafloor habitat and suitable temperatures. With temperature increases above 1.5°C, half of the surface area classified as cusk habitat will disappear, and fragmentation will be further exacerbated at more severe temperature increases (Hare et al., 2012). In addition, the effects of warming on habitat suitability for a species may vary with sex, life stage, and other characteristics, as demonstrated for lobster in the inshore waters of the Gulf of Maine (Tanaka et al., 2018). Finally, while most habitat projections consider individual species in isolation, changes in overlap between predators and prey are also expected to occur as temperatures warm (Selden et al., 2018) and seasonality changes (Pershing et al., 2015; Staudinger et al., 2019). The ability of species to find suitable and sufficient prey and the risks they may face from changing predator fields can both affect the habitats they actually occupy and their potential population productivity (Staudinger et al., 2021). Thus, there is the potential for novel mixes of species, a concern highlighted in the recent U.S. National Climate Assessment (Lipton et al., 2018; Pershing et al., 2018a; Weiskopf et al., 2020).

Commercial fishing has a long history in the Gulf of Maine, and fishing remains one of the most tangible services provided by this ecosystem. Until recent decades, Atlantic cod was the mainstay of the fisheries in this region. Cod occurrence declines dramatically when bottom temperatures exceed 12°C (Drinkwater, 2005; Fogarty et al., 2008). The 1–2°C increase in bottom temperature in the Brickman et al. (2021) projections implies that this threshold will be exceeded on Georges Bank in 2050.

Cod recruitment in the Gulf of Maine and Georges Bank declines with increasing temperature (Drinkwater, 2005; Fogarty et al., 2008; Pershing et al., 2015). With an increase of 3°C, the stocks in Georges Bank, Gulf of Maine, and Browns Bank/Bay of Fundy are all expected to decline, and a 4°C increase is expected to extirpate cod from Georges Bank (Drinkwater, 2005) and possibly the Gulf of Maine (Selden et al., 2018). These higher levels of temperature could occur sporadically during the 2050 climate and more frequently later in the century. More detailed projections suggest that the 1°C increase depicted in the coolest Brickman et al. simulation would reduce the spawning stock biomass of Gulf of Maine cod that produces the maximum sustainable yield to 30,000 mt, slightly more than half the current estimate (Pershing et al., 2015). Warming above 2°C as in the warmest projections for 2050 would reduce the number to 20,000 mt. While much lower than historical production, these values would represent a marked improvement over the estimate that currently there are only 5,000 mt of spawning Gulf of Maine cod. The level of fishing that is sustainable also declines with rising temperature. At 2°C of warming, the stock has been predicted to go extinct at fishing mortality rates in excess of 1.6 yr^{-1}, a level which is sustainable (though far from optimal) under a 1°C increase in temperature (Fogarty et al., 2008).

While cod has traditionally been the most important fishery in the Gulf of Maine, the lobster fishery is currently the most valuable fishery in both the United States and Canada. Le Bris et al. (2018) estimated the future trajectory of lobster in the Gulf of Maine. Their study used the CMIP5 RCP8.5 ensemble, which has temperature changes of 1°C to 2°C by 2050. At these levels of warming, lobster abundance in the Gulf of Maine will decline 42%–62% relative to the recent peak in abundance. This decline would imply a scale of the fishery similar to what existed around 2000. However, the spatial distribution could be different, with higher recruitment in the eastern Gulf of Maine/Bay of Fundy and reduced recruitment in the western Gulf of Maine and on the Scotian Shelf.

As climate drives shifts in the spatial distribution of predators relative to their prey, trophic interactions will likely amplify the direct effects of climate warming. Under a CO_2 doubling scenario (e.g., Saba et al., 2016), spiny dogfish (*S. acanthias*) and silver hake (*M. bilinearis*) are predicted to expand their range over the Northeast Shelf, including in the Gulf of Maine. Range expansion of these predators would result in enhanced overlap with prey, likely increasing their relative importance and replacing cod as piscivores in the U.S. Northeast Shelf ecosystem (Selden et al., 2018). For the next 50 years, the combined climate effects associated with changes in temperature (increasing by about 1°C), pH, oxygen, decreased primary productivity, and shifts in zooplankton size structure, the western Scotian Shelf is projected to experience a reduction in biomass of 19%–29%, an associated decrease in catches of 20%–22%, and a 50% decrease in exploitation rate (Guénette et al., 2014).

Changes in suitable thermal habitat of important commercially fished species will impact local fishing communities and may affect major fishing ports (Colburn et al., 2016; Kleisner et al., 2017). Assessments of fishing community vulnerability to changes in their target species indicate that many communities in the U.S. portion of the Gulf of Maine will experience declines in future fishing opportunities based on current fishing patterns by mid-century (Colburn et al., 2016; Rogers et al., 2019). However, risk is not shared equally among communities. For example, small trawlers in Maine are more vulnerable than other gear types because of their historical dependence on species that are expected to lose habitat suitability in the future, such as Atlantic cod and witch flounder (Rogers et al., 2019). In general, communities that are highly dependent on a low diversity of species—characteristics of many Gulf of Maine fishing

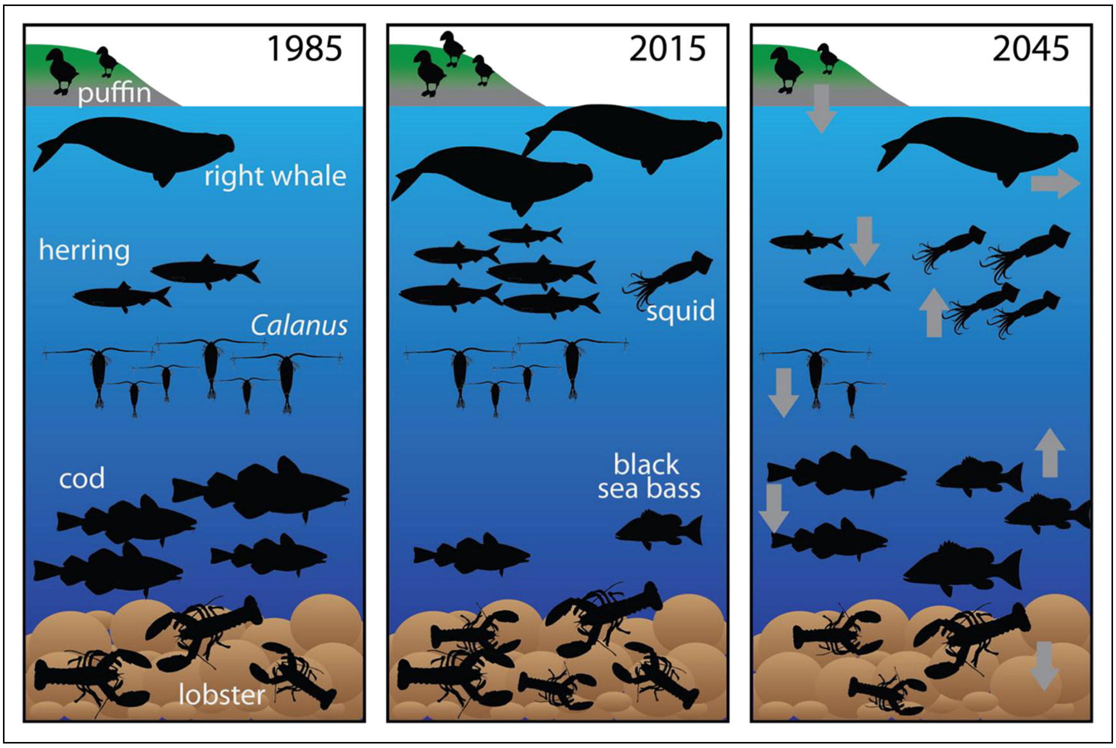

Figure 4. Schematic of the past, present, and future of the Gulf of Maine ecosystem. The graphic depicts the ecosystem circa 1985 (left) and 2015 (center) and plausible conditions in 2050 (right). While conditions were cool in 1985, several subpolar species including herring, right whales, and puffin were at low levels due to human actions and natural variability. By 2015, several temperate species depicted by squid and black sea bass were becoming more common in the Gulf of Maine. Under a moderate warming scenario, many of the subpolar species will have declined and will be declining (down arrows), while temperate species are increasing. If laws in the United States and Canada are followed, right whale abundance should be increasing, but they will likely be moving out of the Gulf of Maine (horizontal arrow). Note that the numbers of icons are not tied to any quantitative assessment but are meant to show only relative change between time periods. DOI: https://doi.org/10.1525/elementa.2020.00076.f4

communities—are expected to be at greatest risk of negative impacts associated with climate change (Colburn et al., 2016). Even communities with fisheries that may benefit from warming can be impacted by climate change in other ways. For example, lobster fishing communities in Atlantic Canada are projected to experience increases in lobster, but vulnerabilities to other climate-related factors, such as sea level rise, will shape community impacts and adaptation needs (Greenan et al., 2019).

Fishers view warming waters as associated with decreased fishing opportunities, indicating that fishing communities are currently finding the prospect of climate adaptation difficult (McClenachan et al., 2019a). However, many do have plans to adapt. For example, Maine lobster fishers indicated that strategies for adaptation include fisheries diversification; supplementing income with non-fishing activities; changing gear use, location, or timing; and becoming more involved in fisheries management and local politics (McClenachan et al., 2019b). However, adaptation is constrained by social, economic, and historical factors (Pinsky and Fogarty, 2012). For example, only 12% of Maine fishers have license holdings that would allow them to access species that are emerging in the Gulf of Maine now and projected to increase in the future (Stoll et al., 2017).

For sustainable commercial fisheries management, warming-induced distribution shifts, productivity changes, and diversity trends should be closely monitored. At the population level, simulation studies show that changes in mortality rates exert particularly strong effects on spawning biomass and catch targets, while maturity and recruitment also influence fishing mortality targets (Thorson et al., 2015). Incorporating both fishing and climate impacts will be important when evaluating the efficacy of management strategies and developing novel solutions to emerging problems. In addition, as climate change impacts transboundary species distributions and access by neighboring coastal communities in Canada and the United States, effective bilateral cooperation between scientists and fishery managers in the two countries is required in the pursuit of sustainable fisheries in the Gulf of Maine (VanderZwaag et al., 2017).

Interdisciplinary case studies

The description above highlights the potential impact of warming on important species or components of the ecosystems (depicted in **Figure 4**). Here, we consider four case studies that emphasize connections within the ecosystem or between the ecosystem and people. These case studies were presented as socio-ecological scenarios for

Gulf of Maine 2050 Symposium participants to envision how the ecosystem might look in 30 years.

Case study: Seabirds

A variety of seabirds nest in large colonies during summer on nearshore and offshore islands located along the Gulf of Maine coastline. Notable species include common, roseate, Arctic, and least terns (*Sterna* sp.) and alcids such as Atlantic puffins (*Fratercula arctica*) and razorbills (*Alca torda*). Seabirds remain close to these islands during the critical period when they breed and raise their young. They are therefore highly dependent on the timing and spatial occurrence of forage resources around these islands as they can only hunt within a limited radius to provision food for their growing chicks. For many of these species, the Gulf of Maine is the southern edge of their biogeographic range.

Long-term diet data of common, roseate, Arctic, and least terns (*Sterna* sp.) show that they have specialized historically on a few key forage fishes, including sand lance, Atlantic herring, and hake (*Urophycis* sp., *Merluccius* sp., and *Enchelyopus* sp.; Hall et al., 2000; Yakola, 2019). This specialization makes these species more vulnerable to shifts in foraging conditions mediated by climate change. Over the last 30 years, at most locations, hake have been generally declining in common tern diets, while sand lance has been increasing at varying magnitudes. The occurrence of hake in common tern diets appears to be most sensitive to changes in seasonal timing (earlier onset of spring) and seasonal sea surface temperatures (Yakola, 2019).

Atlantic puffins act as a tourism magnet wherever they occur and support a substantial bird watching industry, especially in Maine. Puffin breeding phenology is sensitive to sea surface temperature at a North Atlantic scale (Diamond and Devlin, 2003). Puffin chick diets have changed significantly since 2000 (Scopel et al., 2019), corresponding with reductions in a variety of demographic indicators (occupancy, breeding success, chick growth, and fledging condition) since 2005 in eastern (Whidden, 2016; Diamond, 2017) and 2010 in western colonies (Kress et al., 2016). A shift in 2010 to generally warmwater prey coincided with a shift in plankton communities, nutrient concentrations, increased stratification, and above-average ocean temperatures on the Scotian Shelf at the entrance to the Gulf of Maine (Johnson et al., 2018). Juvenile herring dominated puffin diets in the late 1990s but were largely replaced by sand lance (*Ammodytes* spp.), often as larvae, and white hake, and since 2010 by juvenile haddock (*M. aeglefinus*) and Acadian redfish (*S. fasciatus*).

Temperatures in 2012–2013 and 2016 were close to 2°C above normal, roughly the anomaly expected in 2050, allowing experiences in these years to be used as an analogue for 2050. Breeding success was catastrophically low in 2013 and 2016 (Kress et al., 2016; Scopel et al., 2019). Prey availability and puffin hunting abilities are clearly important; as temperatures increase, prey will move into deeper waters to find thermal refuge (Pinsky et al., 2013) and can be more difficult for puffins to catch because fish increase their burst speed in warmer water (Cairns 1998; Grady et al., 2019). Reduced breeding success and condition of fledgling chicks is a potential consequence that can reduce the recruitment of young. As long-lived birds with high annual survival (89%–96%; Breton and Diamond, 2014) populations may not decline measurably for some time despite extremely low reproductive success.

Case study: Lobsters

American lobster supports commercial fisheries worth over $US1.2 billion in the Northeast United States and Maritime Canada (2016 values in $US: Fisheries and Oceans Canada, 2019; NOAA Fisheries, 2019). These fisheries provide income and sustain cultural identities for many small coastal communities. Rising ocean temperatures have affected the productivity, abundance, and distribution of American lobster. In the United States, warming ocean waters have contributed to declines in southern New England and increases in Gulf of Maine lobster populations (Le Bris et al., 2018). These divergent trajectories have been attributed to a reduction in thermal habitat for juvenile lobsters (<20°C) in the south and an expansion in the Gulf of Maine (Steneck and Wahle, 2013; Wahle et al., 2015; Tanaka and Chen, 2016), increased prevalence of epizootic shell disease in the south (Glenn and Pugh, 2006; Oppenheim et al., 2019), and a northward shift in recruitment success (Le Bris et al., 2018; Goode et al., 2019). As a result of changes in productivity and abundance, the centroid of the spatial distribution of American lobster has shifted northward (Pinsky et al., 2013).

While warming trends have influenced the population dynamics of lobster, lobster fisheries were also substantially affected by a marine heat wave in 2012. During this heat wave, sea surface temperature was 1°C–3°C warmer than the long-term average—and on par with end-of-century climate projections (Mills et al., 2013). As temperatures warmed earlier in the spring, high-volume landings in the U.S. fishery began so early that they overlapped with the Canadian lobster season. Transportation and processing capacity could not keep pace with landings, and ultimately, a flood of product led to a price collapse that affected both U.S. and Canadian fisheries (Mills et al., 2013).

Empirical species distribution models give a range of predictions for how lobster distribution may change in the future. Multiple species distribution models indicate that suitable thermal habitat for lobsters in Gulf of Maine and Canadian Maritime waters will increase (Shackell et al., 2014; Kleisner et al., 2017; Morley et al., 2018; Greenan et al., 2019; Tanaka et al., 2020), but one study projects modest biomass declines over the distribution of lobster in the Gulf of Maine (Allyn et al., 2020). These studies vary substantially in the data sources and algorithms used to build and validate the models and in the warming scenarios used. Despite these differences, they generally project distribution shifts of lobster toward the north and into deeper offshore waters under future conditions. To date, the only population projection for lobster that explicitly considers temperature effects on growth, mortality, and recruitment shows that with continued warming, the Gulf of Maine lobster population is projected to decline by approximately 50% between now and 2050 under the mean warming associated with the RCP 8.5 climate scenario (Le Bris et al., 2018). Given the economic and cultural importance of this fishery, reconciling these different views of the future of lobster in the Gulf of Maine should be a high priority.

Case study: Squid

The longfin squid and shortfin squid (*Illex illecebrosus*) have supported important fisheries from Cape Hatteras to Cape Cod for decades (Arkhipkin et al., 2015). Squid fisheries are notoriously "boom and bust" due to the species' sensitivity to environmental and ecosystem conditions (Rodhouse et al., 2014). Distribution and abundance of both species varies from year to year along the continental shelf (Black et al., 1987) and have been linked to water temperature and circulation at multiple spatiotemporal scales (Dawe et al., 2007; Manderson et al., 2011).

Longfin squid have experienced episodic northward distributional shifts in the past (Dow, 1977; Dawe et al., 2007), and in recent years, they have been occurring in harvestable abundances northward of the historical range of the fishery, including within the Gulf of Maine during very warm years (Mills et al., 2013). Shortfin squid landings nearly quadrupled between 2016 and 2017 and have remained relatively high since (NOAA Fisheries, 2019), and fishermen and beachgoers have reported large numbers of the species in nearshore waters and stranded on beaches in the Gulf of Maine (O. Nichols, personal communication, 2019). This increased abundance is also reflected in the diets of many commercially important large pelagic fishes (e.g., tunas) that forage in offshore and Gulf Stream waters (Teffer et al., 2015). We note that this study did not include data after 2010. Given the reported increase in squid in this region, they may likely be an even more important part of the diet of predators.

In general, warming temperatures associated with climate change can be beneficial for squid populations due to plasticity in life history and temperature-dependent growth (provided there is no limitation in food). Notably, many squid species are able to rapidly shift their distributions in response to warming. The sudden appearance of longfin squid in the Gulf of Maine during the 2012 heat wave is similar to the rapid northward expansion of Humboldt squid during El Niño conditions (Zeidberg and Robison, 2007) as well as the episodic northward range extensions of the sympatric *Doryteuthis opalescens* along the U.S. West Coast (Wing and Mercer, 1990). Squids have also expanded northward in the northeast Atlantic (van der Kooij et al., 2016).

Increases in squid abundance in the Gulf of Maine will have implications for both predators and prey. Predicting the future ecological role of squids in the Gulf of Maine ecosystem is difficult, but they serve as a conduit between upper and lower trophic levels and are important as forage for a variety of marine species, including many of commercial importance (Staudinger, 2006; Staudinger and Juanes, 2010; Teffer et al., 2015) as well as of conservation concern (Staudinger, 2006; Staudinger et al., 2014). In bioenergetics terms, smaller squid function optimally at higher temperatures (Pecl and Jackson, 2008), while in a trophodynamics context, larger squid tend to demonstrate higher rates of piscivory and have the potential to exert strong top-down control on prey populations (Hunsicker and Essington, 2006). Predators that benefit from increased temperatures through increased consumption rates, like squid, can have major impacts on food webs and raise concerns for their potential to cause trophic cascades. An updated analysis of consumption of squid and other major prey groups using long-term food habits data series (e.g., Northeast Fisheries Science Center bottom trawl; Smith and Link, 2010) could provide additional insights into recent trends.

The primary means of squid harvest is small-mesh trawl gear, which can result in high levels of bycatch (Hendrickson, 2011). Should squid distribution shift further into the Gulf of Maine, this may present new fishery management challenges, including the need to manage bycatch in the squid fishery. Squid processing requires substantial shoreside infrastructure, of which there is currently little in Gulf of Maine ports. Expansion of squid fishing in this region will require new investments in such infrastructure to adapt and take advantage of future regional increases in this species that is likely to benefit from continued warming.

Case study: Right whales

North Atlantic right whales (*E. glacialis*) are among the most endangered marine mammals in the world, with only around 400 individuals remaining (Pettis et al., 2018). Marine mammal surveys (Cetacean and Turtle Assessment Program, 1982; Mayo et al., 2004; Brown et al., 2007; Cole et al., 2007) established that all core right whale feeding habitats are in and around the Gulf of Maine. Ecosystem studies have revealed that the predictable seasonal occurrence of right whales is linked to high concentrations of their prey, the lipid-rich *Calanus* and other copepods (Mayo and Marx, 1990; Baumgartner et al., 2003; Pendleton et al., 2009). Recovery efforts have focused on reducing human-caused mortality due to ship strikes and fishing gear entanglements. Conservation measures have included moving shipping lanes away from right whale core areas, establishing speed limits for large vessels, and modifying fishing gear. These measures have been applied in a manner that follows the annual migratory path of right whales, from one Gulf of Maine feeding habitat to another. Reduced mortality due to improved management (Laist et al., 2014) and increased calf production associated with elevated *Calanus* abundance (e.g., Meyer-Gutbrod et al., 2015) allowed the population to build from 350 whales in the late 1990s to over 400 whales.

In 2010, a shift occurred. Right whale occurrences in the Bay of Fundy feeding habitat in the eastern Gulf of Maine dropped sharply (Davis et al., 2017). The drop in right whales coincided with a decline in *Calanus* in the eastern Gulf of Maine, which was strongly correlated with warming in deep waters entering through the Northeast Channel beginning in 2010 (Record et al., 2019b). These climate-driven circulation changes have undermined a previously reliable feeding habitat for right whales. The right whale population has responded by moving to other areas during this time of year, presumably to find other feeding grounds. Their appearance in areas where protective measures are not in place, such as the Gulf of St. Lawrence, has led to a sharp increase in mortalities (Davies and Brilliant, 2019). Meanwhile, calving rates have also declined, as whales struggle to find new feeding grounds (Meyer-Gutbrod and Greene, 2018). The result is that since 2010, after many years of slow population growth, the right whale population has been in steady decline (Kraus et al., 2016; Pace et al., 2017).

Maintaining right whale protections as conditions change is a challenge. The loss of a reliable seasonality to their habitat use has made management actions reactive rather than proactive. Protective measures sometimes have economic impacts on fisheries, such as the New England lobster fishery, and management now requires more international cooperation than ever before. At the same time, whales are not simply following an isotherm, but rather hunting for good feeding grounds, which depend on temperature, ocean productivity, and complex currents. For example, a new spring feeding ground has appeared in southern New England likely focused on the same coastal copepod community that draws whales to Cape Cod Bay (e.g., Pendleton et al., 2012).

Warming has already impacted right whale management, and continued warming is likely to amplify the management challenges. Projections of right whale distributions for the year 2050, based on projected climate variables and *Calanus* distributions, show a probable decline in right whale habitat suitability across most of the Gulf of Maine, at least for summer and fall months (Ross et al., 2021). Under continued warming, right whales may continue to expand their feeding areas into the Gulf of St. Lawrence and potentially the Newfoundland Shelf and other parts of the North Atlantic (e.g., Ramp et al., 2015). However, given the potential for the western Gulf of Maine to act as refugia for *Calanus* (Runge et al., 2015) and the recent expansion into southern New England, managing right whales will not be as simple as shifting protections to the north.

Despite the challenges facing right whales, recovery is still possible, even under strong warming, provided direct human-caused mortality is severely curtailed (Meyer-Gutbrod and Greene, 2018). For the right whale population to recover, management protections will need to cover the entire range of the species, which will need to be established and adjusted. These protections could be refined through dynamic management strategies (e.g., Pendleton et al., 2012; Becker et al., 2016). Crucially, these measures will need to include changes to shipping and fishing practices to reduce their impact on right whales.

Conclusions

The resulting environmental and ecological changes described in this article have implications for the ecosystem services that human communities and economies around the Gulf of Maine depend on for food, livelihoods, recreation, heritage, and culture. Changes in the timing, distribution, and abundance of commercially and recreationally important populations will affect their availability to the fishing industry, in many cases, increase costs of operations (e.g., the distance and associated costs to travel offshore to find and harvest the species). However, increased availability of warmwater species such as black sea bass, summer flounder, and longfin squid could provide new markets for fishing communities if state and regional policies are able to adapt to facilitate harvesting opportunities where and when they occur relative to fishing ports.

Recreational and tourism industries will also experience changes based on whether certain activities diminish or increase in duration (or are eliminated completely) due to changing seasonal conditions. For example, ice fishing for species like smelt may become less profitable as ice cover decreases and reduces the time when activities can occur. Conversely, wildlife viewing (e.g., whale watching and seabirds) and recreational fishing opportunities may increase with more pleasant summer and fall conditions lasting longer. Still, if species of interest move out of traditional areas and away from the region or if their populations decline due to changes in forage and thermal habitats, declines or shifts in tourism and recreational opportunities may occur.

Importantly, tribal nations and other coastal communities that depend on climate-affected species will suffer due to losses of economic and subsistence harvests (Jantarasami et al., 2018). While possibilities remain for communities to shift to new (warmwater associated) species as they move into the region, many communities that identify with certain species or places will experience a loss of heritage and culture that can further impact human health and well-being in the region (Daigle et al., 2019).

Data accessibility statement

All data reported in this article come from publicly available sources (e.g., the NOAA database on extended reconstruction sea surface temperature at https://www.ncdc.noaa.gov/data-access/marineocean-data/extended-reconstructed-sea-surface-temperature-ersst-v5) or are published elsewhere (e.g., Brickman et al., 2021), as cited in the text.

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Competing interests

The authors have no competing interests to declare.

Author contributions

Organized the conceptualization and execution of the article: AJP.

Drafted and/or revised the article: All authors.

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References

Alexander, MA, Shin, S-i, Scott, JD, Curchitser, E, Stock, C. 2020. The response of the northwest Atlantic Ocean to climate change. *Journal of Climate* **33**(2): 405–428.

Allyn, AJ, Alexander, MA, Franklin, BS, Massiot-Granier, F, Pershing, AJ, Scott, JD, Mills, KE. 2020. Comparing and synthesizing quantitative distribution models and qualitative vulnerability assessments to project marine species distributions under climate change. *PLoS One* **15**(4): e0231595. DOI: http://dx.doi.org/10.1371/journal.pone.0231595.

Arkhipkin, AI, Rodhouse, PGK, Pierce, GJ, Sauer, W, Sakai, M, Allcock, L, Arguelles, J, Bower, JR, Castillo, G, Ceriola, L, Chen, CS. 2015. World squid fisheries. *Reviews in Fisheries Science & Aquaculture* **23**(2): 92–252.

Baumgartner, MF, Cole, TVN, Campbell, RG, Teegarden, GJ, Durbin, EG. 2003. Associations between North Atlantic right whales and their prey, *Calanus finmarchicus*, over diel and tidal time scales. *Marine Ecology Progress Series* **264**: 155–166.

Becker, E, Forney, K, Fiedler, P, Barlow, J, Chivers, S, Edwards, C, Moore, A, Redfern, J. 2016. Moving towards dynamic ocean management: How well do modeled ocean products predict species distributions? *Remote Sensing* **8**: 149.

Beever, EA, O'Leary, J, Mengelt, C, West, JM, Julius, S, Green, N, Magness, D, Petes, L, Stein, B, Nicotra, AB, Hellmann, JJ. 2016. Improving conservation outcomes with a new paradigm for understanding species' fundamental and realized adaptive capacity. *Conservation Letters* **9**(2): 131–137.

Belknap, DF, Wilson, KR. 2015, March 23–25. Effects of invasive green crabs on salt marshes in Maine. Geological Society of America Meeting, Portland, ME.

Bernier, RY, Jamieson, RE, Moore, AM. 2018. State of the Atlantic ocean synthesis report. *Canadian Technical Report of Fisheries and Aquatic Sciences* **3167**: iii + 149.

Black, GAP, Rowell, TW, Dawe, EG. 1987. Atlas of the biology and distribution of the squids *Illex illecebrosus* and *Loligo pealei* in the Northwest Atlantic. *Canadian Special Publication of Fisheries and Aquatic Sciences* **100**: 62.

Breton, AR, Diamond, AW. 2014. Annual survival of adult Atlantic Puffins *Fratercula arctica* is positively correlated with Herring *Clupea harengus* availability. *Ibis* **156**(1): 35–47.

Brickman, D, Alexander, MA, Pershing, AJ, Scott, JD, Wang, Z. 2021. Projections of physical conditions in the Gulf of Maine in 2050. *Elementa: Science of the Anthropocene* **9**(1): 00055. DOI: http://dx.doi.org/10.1525/elementa.2020.20.00055.

Brickman, D, Hebert, D, Wang, Z. 2018. Mechanism for the recent ocean warming events on the Scotian Shelf of Eastern Canada. *Continental Shelf Research* **156**: 11–22.

Brickman, D, Wang, Z, DeTracey, B. 2016. High resolution future climate ocean model simulations for the Northwest Atlantic shelf region. *Canadian Technical Report of Fisheries and Aquatic Sciences* **315**: 1–143.

Brown, MW, Kraus, SD, Slay, CK, Garrison, LP. 2007. Surveying for discovery, science, and management, in Kraus, SD, Rolland, RM eds., *The urban whale: North Atlantic right whales at the crossroads*. Cambridge, MA: Harvard University Press: 105–137.

Caesar, L, Rahmstorf, S, Robinson, A, Feulner, G, Saba, V. 2018. Observed fingerprint of a weakening Atlantic Ocean overturning circulation. *Nature* **556**: 191–196.

Cairns, DK. 1988. Seabirds as indicators of marine food supplies. *Biological Oceanography* **5**(4): 261–271.

Cetacean and Turtle Assessment Program. 1982. A characterization of marine mammals and turtles in the mid- and North-Atlantic areas of the U.S. outer continental shelf. Final report, Contract No. AA551-CT8–48. Washington, DC: Bureau of Land Management.

Charif, RA, Shiu, Y, Muirhead, CA, Clark, CW, Parks, SE, Rice, AN. 2020. Phenological changes in North Atlantic right whale habitat use in Massachusetts Bay. *Global Change Biology* **26**: 734–745.

Chisholm, L, Talbot, T, Appleby, W. 2021. Projected weather and sea level for the Gulf of Maine region. *Elementa: Science of the Anthropocene* **9**(1): 00059. DOI: https://doi.org/10.1525/elementa.2021.00059.

Clark, S, Hubbard, KA, Anderson, DM, McGillicuddy, DJ, Ralston, DK, Townsend, DW. 2019. *Pseudo-nitzschia* bloom dynamics in the Gulf of Maine: 2012–2016. *Harmful Algae* **88**: 101656.

Colburn, LL, Jepson, M, Weng, C, Seara, T, Weiss, J, Hare, JA. 2016. Indicators of climate change and social vulnerability in fishing dependent communities along the Eastern and Gulf Coasts of the United States. *Marine Policy* **74**: 323–333. DOI: http://dx.doi.org/10.1016/j.marpol.2016.04.030.

Cole, TVN, Gerrior, P, Merrick, RL. 2007. *Methodologies and preliminary results of the NOAA National Marine Fisheries Service aerial survey program for right whales (Eubalaena glacialis) in the northeast U.S., 1998–2006. Northeast Fisheries Science Center Reference Document 07–02.* Woods Hole, MA: National Marine Fisheries Service.

Congleton, WR. 2006. Trends in Maine softshell clam landing. *Journal of Shellfish Research* **25**: 475–480.

Daigle, J, Michelle, N, Ranco, D, Emery, M. 2019. Traditional lifeways and storytelling: Tools for adaptation and resilience to ecosystem change. *Human Ecology* **47**(5): 777–784.

Davies, KTA, Brillant, SW. 2019. Mass human-caused mortality spurs federal action to protect endangered North Atlantic right whales in Canada. *Marine Policy* **104**: 157–162.

Davis, GE, Baumgartner, MF, Bonnell, JM, Bell, J, Berchok, C, Thornton, JB, Brault, S, Buchanan, G, Charif, RA, Cholewiak, D, Clark, CW. 2017.

Long-term passive acoustic recordings track the changing distribution of North Atlantic right whales (*Eubalaena glacialis*) from 2004 to 2014. *Scientific Reports* **7**(1): 1–12.

Dawe, EG, Hendrickson, LC, Colbourne, EB, Drinkwater, KF, Showell, MA. 2007. Ocean climate effects on the relative abundance of short-finned (*Illex illecebrosus*) and long-finned (*Loligo pealeii*) squid in the northwest Atlantic Ocean. *Fisheries Oceanography* **16**: 303–316.

de la Riva, GT, Johnson, CK, Gulland, FM, Langlois, GW, Heyning, JE, Rowles, TK, Mazet, JA. 2009. Association of an unusual marine mammal mortality event with *Pseudo-nitzschia* spp. blooms along the southern California coastline. *Journal of Wildlife Diseases* **45**(1): 109–121. Available at https://www.ncbi.nlm.nih.gov/pubmed/19204340.

Diamond, AW. 2017. Birds in a warming world: What can we expect? *NB Naturalist* **44**(3): 23–25.

Diamond, AW, Devlin, CM. 2003. Seabirds as indicators of changes in marine ecosystems: Ecological monitoring on Machias Seal Island. *Environmental Monitoring and Assessment* **88**(1): 153–181. DOI: http://dx.doi.org/10.1023/A:1025560805788.

Dijkstra, J, Harris, LG, Westerman, E. 2007. Distribution and long-term temporal patterns of four invasive colonial ascidians in the Gulf of Maine. *Journal of Experimental Marine Biology and Ecology* **342**(1): 61–68.

Dow, RL. 1977. Effects of climatic cycles on the relative abundance and availability of commercial marine and estuarine species. *Journal du Conseil International pour l'Exploration de la Mer* **37**: 274–280.

Drinkwater, KF. 2005. The response of Atlantic cod (*Gadus morhua*) to future climate change. *Ices Journal of Marine Science* **62**: 1327–1337.

Fernandez, I, Schmitt, C, Stancioff, E, Birkel, S, Pershing, A, Runge, J, Jacobson, G, Mayewski, P. 2015. Maine's climate future: 2015 Update. Climate Change Institute Faculty Scholarship, No. 5. Available at https://digitalcommons.library.umaine.edu/climate_facpub/5.

Fisheries and Oceans Canada. 2019. Seafisheries landings. 2016 Data. Available at http://www.dfo-mpo.gc.ca/stats/commercial/sea-maritimes-eng.htm. Accessed 26 August 2019.

Fogarty, M, Incze, L, Hayhoe, K, Mountain, D, Manning, J. 2008. Potential climate change impacts on Atlantic cod (*Gadus morhua*) off the Northeastern United States. *Mitigation and Adaptation Strategies for Global Change* **13**: 453–466.

Glenn, RP, Pugh, TL. 2006. Epizootic shell disease in American lobster (*Homarus americanus*) in Massachusetts coastal waters: Interactions of temperature, maturity, and intermolt duration. *Journal of Crustacean Biology* **26**: 639–645.

Glude, JB. 1955. The effects of temperature and predators on the abundance of soft-shell clam, *Mya arenaria*, in New England. *Transactions of the American Fisheries Society* **84**: 13–26.

Golet, WJ, Record, NR, Lehuta, S, Lutcavage, M, Galuardi, B, Cooper, AB, Pershing, AJ. 2015. The paradox of the pelagics: Why bluefin tuna can go hungry in a sea of plenty. *Marine Ecology Progress Series* **527**: 181–192.

Goode, A, Brady, DC, Steneck, RS, Wahle, RA. 2019. The brighter side of climate change: Ocean warming crosses a biological threshold to amplify an iconic fishery. *Global Change Biology* **25**: 3906–3917. DOI: http://dx.doi.org/10.1111/gcb.14778.

Grady, JM, Maitner, BS, Winter, AS, Kaschner, K, Tittensor, DP, Record, S, Smith, FA, Wilson, AM, Dell, AI, Zarnetske, PL, Wearing, HJ, Alfaro, B, Brown, JH. 2019. Metabolic asymmetry and the global diversity of marine predators. *Science* **363**(6425): eaat4220.

Greenan, BJW, Shackell, NL, Ferguson, K, Grayson, P, Cogswell, A, Brickman, D, Wang, Z, Cook, A, Breenan, CE, Saba, VS. 2019. Climate change vulnerability of American lobster fishing communities in Atlantic Canada. *Frontiers in Marine Science.* DOI: http://dx.doi.org/10.3389/fmars.2019.00579.

Grieve, BD, Hare, JA, Saba, VS. 2017. Projecting the effects of climate change on *Calanus finmarchicus* distribution within the US Northeast Continental Shelf. *Scientific Reports* **7**(1): 1–12.

Griffen, BD, Riley, ME. 2015. Potential impacts of invasive crabs on the life history strategy of native rock crabs in the Gulf of Maine. *Biological Invasions* **17**: 2533–2544.

Griffin, LP, Griffin, CR, Finn, JT, Prescott, RL, Faherty, M, Still, BM, Danylchuk, AJ. 2019. Warming seas increase cold-stunning events for Kemp's Ridley sea turtles in the northwest Atlantic. *PLoS One* **14**(1): e0211503.

Guenette, S, Araújo, JN, Bundy, A. 2014. Exploring the potential effects of climate change on the Western Scotian Shelf ecosystem. *Canadian Journal of Marine Systems* **134**: 89–100. DOI: http://dx.doi.org/10.1016/j.jmarsys.2014.03.001.

Hall, CS, Kress, SW, Griffin, CR. 2000. Composition, spatial and temporal variation of Common and Arctic Tern chick diets in the Gulf of Maine. *Waterbirds* **23**: 430–439.

Hare, JA, Manderson, JP, Nye, JA, Alexander, MA, Auster, PJ, Borggaard, DL, Capotondi, AM, Damon-Randall, KB, Heupel, E, Mateo, I, O'Brien, L. 2012. Cusk (*Brosme brosme*) and climate change: Assessing the threat to a candidate marine fish species under the US Endangered Species Act. *ICES Journal of Marine Science* **69**: 1753–1768.

Hare, JA, Morrison, WE, Nelson, MW, Stachura, MM, Teeters, EJ, Griffis, RB, Alexander, MA, Scott, JD, Alade, L, Bell, RJ, Chute, AS. 2016. A vulnerability assessment of fish and invertebrates to climate change on the Northeast US Continental Shelf. *PLoS One* **11**(2): e0146756.

Hendrickson, LC. 2011. Effects of a codend mesh size increase on size selectivity and catch rates in a small-mesh bottom trawl fishery for longfin inshore squid, *Loligo pealeii. Fisheries Research* **108**: 42–51.

Hodgkins, GA, Dudley, RW, Huntington, TG. 2003. Changes in the timing of high river flows in New England over the 20th century. *Journal of Hydrology* **278**(1–4): 244–252. DOI: http://dx.doi.org/10.1016/S0022-1694(03)00155-0.

Hunsicker, ME, Essington, TE. 2006. Size-structured patterns of piscivory of the longfin inshore squid (*Loligo pealeii*) in the mid-Atlantic continental shelf ecosystem. *Canadian Journal of Fisheries and Aquatic Sciences* **63**(4): 754–765.

Huntington, TG, Billmire, M. 2014. Trends in precipitation, runoff, and evapotranspiration for rivers draining to the Gulf of Maine in the United States. *Journal of Hydrometeorology* **15**(2): 726–743. DOI: http://dx.doi.org/10.1175/JHM-D-13-018.1.

Jantarasami, LC, Novak, R, Delgado, R, Marino, E, McNeeley, S, Narducci, C, Raymond-Yakoubian, J, Singletary, L, Powys Whyte, K. 2018. Tribes and Indigenous peoples, in Reidmiller, DR, Avery, CW, Easterling, DR, Kunkel, KE, Lewis, KLM, Maycock, TK, Stewart, BC eds., *Impacts, risks, and adaptation in the United States: Fourth national climate assessment* (vol. II). Washington, DC: U.S. Global Change Research Program.

Ji, R, Feng, Z, Jones, BT, Thompson, C, Chen, C, Record, NR, Runge, JA. 2017. Coastal amplification of supply and transport (CAST): A new hypothesis about the persistence of *Calanus finmarchicus* in the Gulf of Maine. *ICES Journal of Marine Science*. DOI: http://dx.doi.org/10.1093/icesjms/fsw253.

Johnson, C, Devred, E, Casault, B, Head, E, Spry, J. 2018. Optical, chemical, and biological oceanographic conditions on the Scotian Shelf and in the Eastern Gulf of Maine in 2016. DFO Canadian Science Advisory Secretariat 2018/017. V, p. 58. Dartmouth, Canada: Department of Fisheries and Oceans.

Johnson, CL, Leising, AW, Runge, JA, Head, EJH, Pepin, P, Plourde, S, Durbin, EG. 2007. Characteristics of *Calanus finmarchicus* dormancy patterns in the Northwest Atlantic. *ICES Journal of Marine Science* **65**: 339–350.

Kleisner, KM, Fogarty, MJ, McGee, S, Barnette, A, Fratantoni, P, Greene, J, Hare, JA, Lucey, SM, McGuire, C, Odell, J, Saba, VS. 2016. The effects of sub-regional climate velocity on the distribution and spatial extent of marine species assemblages. *PLoS One* **11**(2). DOI: http://dx.doi.org/10.1371/journal.pone.0149220.

Kleisner, KM, Fogarty, MJ, McGee, S, Hare, JA, Moret, S, Perretti, CT, Saba, VS. 2017. Marine species distribution shifts on the US Northeast Continental Shelf under continued ocean warming. *Progress in Oceanography* **153**: 24–36.

Kraus, SD, Kenney, RD, Mayo, CA, McLellan, WA, Moore, MJ, Nowacek, DP. 2016. Recent scientific publications cast doubt on North Atlantic right whale future. *Frontiers in Marine Science* **3**: 137.

Kress, SW, Shannon, P, O'Neal, C. 2016. Recent changes in the diet and survival of Atlantic puffin chicks in the face of climate change and commercial fishing in midcoast Maine, USA. *Facets* **1**: 27–43.

Laist, D, Knowlton, A, Pendleton, D. 2014. Effectiveness of mandatory vessel speed limits for protecting North Atlantic right whales. *Endangered Species Research* **23**: 133–147.

Lasley-Rasher, R, Brady, DC, Smith, B, Jumars, PA. 2015. It takes guts to locate mobile crustacean prey. *Marine Ecology Progress Series* **538**: 1–12.

Le Bris, A, Mills, KE, Wahle, RA, Chen, Y, Alexander, MA, Allyn, AJ, Schuetz, JG, Scott, JD, Pershing, AJ. 2018. Climate vulnerability and resilience in the most valuable North American fishery. *Proceedings of the National Academy of Sciences* **115**: 1831–1836.

Li, Y, Fratantoni, PS, Chen, C, Hare, JA, Sun, Y, Beardsley, RC, Ji, R. 2015. Spatio-temporal patterns of stratification on the Northwest Atlantic shelf. *Progress in Oceanography* **134**: 123–137.

Lipton, D, Rubenstein, MA, Weiskopf, SR, Carter, S, Peterson, J, Crozier, L, Fogarty, M, Gaichas, S, Hyde, KJ, Morelli, TL, Morisette, J. 2018. Ecosystems, ecosystem services, and biodiversity, in Reidmiller, DR, Avery, CW, Easterling, DR, Kunkel, KE, Lewis, KLM, Maycock, TK, Stewart, BC eds., *Impacts, risks, and adaptation in the United States: Fourth national climate assessment* (vol. II). Washington, DC: U.S. Global Change Research Program: 268–321.

Loder, JW, Petrie, B, Gawarkiewicz, G. 1998. The coastal ocean off northeastern North America: A large-scale view, in Robinson, AR, Brink, KH eds., *The sea*. New York, NY: John Wiley: 105–133.

Manderson, J, Palamara, L, Kohut, J, Oliver, MJ. 2011. Ocean observatory data are useful for regional habitat modeling of species with different vertical habitat preferences. *Marine Ecology Progress Series* **438**: 1–17.

Marquis, ND, Record, NR, Fernández Robledo, JA. 2015. Survey for protozoan parasites in Eastern oysters (*Crassostrea virginica*) from the Gulf of Maine using PCR-based assays. *Parasitology International* **64**: 299–302.

Mayo, CA, Marx, MK. 1990. Surface foraging behavior of the North Atlantic right whale, *Eubalaena glacialis*, and associated zooplankton characteristics. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **68**: 2214–2220.

Mayo, CA, Nichols, OC, Bessinger, MK, Brown, MW, Marx, MK, Browning, CL. 2004. *Surveillance, monitoring, and management of North Atlantic right whales in Cape Cod Bay and adjacent waters—2004*. Provincetown, MA: Center for Coastal Studies. Final report submitted to the Commonwealth of Massachusetts, Division of Marine Fisheries.

McBride, RS, Tweedie, MK, Oliveira, K. 2018. Reproduction, first-year growth, and expansion of spawning and nursery grounds of black sea bass (*Centropristis *striata*) into a warming Gulf of Maine. *Fishery Bulletin* **116**: 323–336.

McClenachan, L, Grabowski, JH, Marra, M, McKeon, CS, Neal, BP, Record, NR, Scyphers, SB. 2019a. Shifting perceptions of rapid temperature changes' effects on marine fisheries, 1945–2017. *Fish and Fisheries* **20**(6): 1111–1123.

McClenachan, L, Scyphers, S, Grabowski, JH. 2019b. Views from the dock: Warming waters, adaptation, and the future of Maine's lobster fishery. *Ambio* **49**(1): 144–155.

McMahan, MD, Grabowski, JH. 2019. Nonconsumptive effects of a range-expanding predator on juvenile lobster (*Homarus americanus*) population dynamics. *Ecosphere* **10**(10): e02867.

Melle, W, Runge, J, Head, E, Plourde, S, Castellani, C, Licandro, P, Pierson, J, Jonasdottir, S, Johnson, C, Broms, C, Debes, H. 2014. The North Atlantic Ocean as habitat for *Calanus finmarchicus*: Environmental factors and life history traits. *Progress in Oceanography* **129**: 244–284.

MERCINA Working Group. 2001. Oceanographic responses to climate in the Northwest Atlantic. *Oceanography* **14**: 76–82.

Meyer-Gutbrod, EL, Greene, CH. 2018. Uncertain recovery of the North Atlantic right whale in a changing ocean. *Global Change Biology* **24**: 455–464.

Meyer-Gutbrod, EL, Greene, CH, Sullivan, PJ, Pershing, AJ. 2015. Climate-associated changes in prey availability drive reproductive dynamics of the North Atlantic right whale population. *Marine Ecology Progress Series* **535**: 243–258.

Mills, KE, Pershing, AJ, Brown, CJ, Chen, Y, Chiang, F, Holland, DS, Lehuta, S, Nye, JA, Sun, JC, Thomas, AC, Wahle, RA. 2013. Fisheries management in a changing climate: Lessons from the 2012 ocean heat wave in the Northwest Atlantic. *Oceanography* **26**: 191–195.

Moritz, C, Agudo, R. 2013. The future of species under climate change: resilience or decline? *Science* **341**(6145): 504–508.

Morley, JW, Selden, RL, Latour, RJ, Frölicher, TL, Seagraves, RJ, Pinsky, ML. 2018. Projecting shifts in thermal habitat for 686 species on the North American continental shelf. *PLoS One* **13**: e0196127.

Neckles, HA. 2015. Loss of eelgrass in Casco, Bay Maine, linked to green crab disturbance. *Northeastern Naturalist* **22**: 478–500.

NOAA Fisheries. 2019. Commercial landings statistics. Available at https://foss.nmfs.noaa.gov/.

Northeast Fisheries Science Center. 2018. *65th Northeast regional stock assessment workshop (65th SAW) assessment summary report.* Woods Hole, MA: NOAA Northeast Fisheries Science Center.

Nye, JA, Joyce, TM, Kwon, Y-O, Link, JS. 2011. Silver hake tracks changes in Northwest Atlantic circulation. *Nature Communications* **2**(1): 1–6.

Nye, JA, Link, JS, Hare, JA, Overholtz, WJ. 2009. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. *Marine Ecology Progress Series* **393**: 111–129.

Oppenheim, NG, Wahle, RA, Brady, D, Goode, AG, Pershing, AJ. 2019. The cresting wave: Larval settlement and ocean temperatures predict change in the American lobster harvest. *Ecological Applications.* DOI: http://dx.doi.org/10.1002/eap.2006.

Overholtz, WJ, Hare, JA, Keith, CM. 2011. Impacts of interannual environmental forcing and climate change on the distribution of Atlantic mackerel on the U.S. Northeast Continental Shelf. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* **3**(1): 219–232. DOI: http://dx.doi.org/10.1080/19425120.2011.578485.

Pace, RM, Corkeron, PJ, Kraus, SD. 2017. State–space mark–recapture estimates reveal a recent decline in abundance of North Atlantic right whales. *Ecology and Evolution* **7**(21): 8730–8741.

Pecl, GT, Jackson, GD. 2008. The potential impacts of climate change on inshore squid: Biology, ecology and fisheries. *Reviews in Fish Biology and Fisheries* **18**(4): 373–385.

Pendleton, DE, Pershing, AJ, Brown, MW, Mayo, CA, Kenney, RD, Record, RD, Cole, TVN. 2009. Regional scale mean matters: mean copepod concentration indicates relative abundance of North Atlantic right whales. *Marine Ecology Progress Series* **378**: 211–225.

Pendleton, DE, Sullivan, PJ, Brown, MW, Cole, TVN, Good, CP, Mayo, CA, Monger, BC, Phillips, S, Record, NR, Pershing, AJ. 2012. Weekly predictions of North Atlantic right whale *Eubalaena glacialis* habitat reveal influence of prey abundance and seasonality of habitat preferences. *Endangered Species Research* **18**:147–161.

Pershing, AJ, Alexander, MA, Hernandez, CM, Kerr, LA, Le Bris, A, Mills, KE, Nye, JA, Record, NR, Scannell, HA, Scott, JD, Sherwood, GD. 2015. Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. *Science* **350**: 809–812.

Pershing, AJ, Griffis, RB, Jewett, EB, Armstrong, CT, Bruno, JF, Busch, DS, Haynie, AC, Siedlecki, SA, Tommasi, D. 2018a. Oceans and marine resources, in Reidmiller, DR, Avery, CW, Easterling, DR, Kunkel, KE, Lewis, KLM, Maycock, TK, Stewart, BC eds., *Impacts, risks, and adaptation in the United States: Fourth national climate assessment* (vol. II). Washington, DC: U.S. Global Change Research Program: 353–390.

Pershing, AJ, Mills, KE, Dayton, AM, Franklin, BS, Kennedy, BT. 2018b. Evidence for adaptation from the 2016 marine heatwave in the Northwest Atlantic Ocean. *Oceanography* **31**: 152–161.

Pershing, AJ, Stamieszkin, K. 2020. The North Atlantic ecosystem, from plankton to whales. *Annual Review of Marine Science* **12**: 1. DOI: http://dx.doi.org/10.1146/annurev-marine-010419-010752.

Pettis, HM, Pace, RM, Hamilton, PK. 2018. *North Atlantic right whale consortium 2018 annual* *report card*. Boston, MA: North Atlantic Right Whale Consortium.

Pinsky, ML, Fogarty, M. 2012. Lagged social-ecological responses to climate and range shifts in fisheries. *Climate Change* **115**: 883–891.

Pinsky, ML, Worm, B, Fogarty, MJ, Sarmiento, JL, Levin, SA. 2013. Marine taxa track local climate velocities. *Science* **341**: 1239–12342.

Ramp, C, Delarue, J, Palsbøll, PJ, Sears, R, Hammond, PS. 2015. Adapting to a warmer ocean—Seasonal shift of baleen whale movements over three decades. *PLoS One*: 10: e0121374.

Record, NR, Balch, WM, Stamieszkin, K. 2019a. Century-scale changes in phytoplankton phenology in the Gulf of Maine. *PeerJ* **7**: e6735.

Record, NR, Countway, PD, Kanwit, K, Fernández-Robledo, JA. 2021. Rise of the rare biosphere: Thinking beyond climate envelopes for harmful algal blooms. *Elementa: Science of the Anthropocene* **9**(1): 00056. DOI: https://doi.org/10.1525/elementa.2020.00056.

Record, NR, Pershing, AJ, Maps, F. 2013. Emergent copepod communities in an adaptive trait-structured model. *Ecological Modelling* **260**: 11–24.

Record, NR, Runge, JA, Pendleton, DE, Balch, WM, Davies, KTA, Pershing, AJ, Johnson, CL, Stamieszkin, K, Ji, R, Feng, Z, Kraus, SD. 2019b. Rapid climate-driven circulation changes threaten conservation of endangered North Atlantic right whales. *Oceanography* **32**. DOI: http://dx.doi.org/10.5670/oceanog.2019.201.

Reygondeau, G, Beaugrand, G. 2011. Future climate-driven shifts in distribution of *Calanus finmarchicus. Global Change Biology* **17**: 756–766.

Richards, RA. 2012. Phenological shifts in hatch timing of northern shrimp *Pandalus borealis*. *Marine Ecology Progress Series* **456**: 149–158. DOI: http://dx.doi.org/10.3354/meps09717.

Richards, RA, O'Reilly, JE, Hyde, KJW. 2016. Use of satellite data to identify critical periods for early life survival of northern shrimp in the Gulf of Maine. *Fish Ocean* **25**(3): 306–319.

Richards, RA, Whitmore, K, Fischer, J, Hunter, M, Waine, M, Drew, K. 2012. Assessment report for Gulf of Maine northern shrimp—2012. Atlantic States Marine Fisheries Commission's Northern Shrimp Technical Committee. Available at http://www.asmfc.org/uploads/file/2012NorthernShrimpAssessment.pdf.

Robledo, JAF, Marquis, ND, Countway, PD, Record, NR, Irish, EL, Schuldt, MM, Kingston, SE, Bishop, TJ, Messerman, NA, Bowden, TJ. 2018. Pathogens of marine bivalves in Maine (USA): A historical perspective. *Aquaculture* **493**: 9–17.

Rodhouse, PGK, Pierce, GJ, Nichols, OC, Sauer, WHH, Arkhipkin, AI, Laptikhovsky, VV, Lipiński, MR, Ramos, JE, Gras, M, Kidokoro, H, Sadayasu, K. 2014. Environmental effects on cephalopod population dynamics: implications for management of fisheries. *Advances in Marine Biology* **67**: 99–233.

Rogers, LA, Griffin, R, Young, T, Fuller, E, Martin, KS, Pinsky, ML. 2019. Shifting habitats expose fishing communities to risk under climate change. *Nature Climate Change* **9**: 512–516.

Ross, CH, Record, NR, Pendleton, DE, Tupper, B, Brickman, D. 2021. Predicting regions of North Atlantic right whale, *Eubalaena glacialis*, habitat suitability in the Gulf of Maine in 2050. *Elementa: Science of the Anthropocene* **9**(1): 00058. DOI: http://dx.doi.org/10.1525/elementa.2020.20.00058.

Runge, JA, Ji, RB, Thompson, CRS, Record, NR, Chen, CS, Vandemark, DC, Salisbury, JE, Maps, F. 2015. Persistence of *Calanus finmarchicus* in the western Gulf of Maine during recent extreme warming. *Journal of Plankton Research* **37**: 221–232.

Saba, VS, Griffies, SM, Anderson, WG, Winton, M, Alexander, MA, Delworth, TL, Hare, JA, Harrison, MJ, Rosati, A, Vecchi, GA, Zhang, R. 2016. Enhanced warming of the Northwest Atlantic Ocean under climate change. *Journal of Geophysical Research: Oceans* **121**(1): 118–132. DOI: http://dx.doi.org/10.1002/2015jc011346.

Scopel, L, Diamond, A, Kress, S, Shannon, P. 2019. Varied breeding responses of seabirds to a regime shift in prey base in the Gulf of Maine. *Marine Ecology Progress Series* **626**: 177–196.

Selden, RL, Batt, RD, Saba, VS, Pinsky, ML. 2018. Diversity in thermal affinity among key piscivores buffers impacts of ocean warming on predator–prey interactions. *Global Change Biology* **24**: 117–131.

Shackell, NL, Ricard, D, Stortini, C. 2014. Thermal habitat index of many Northwest Atlantic temperate species stays neutral under warming projected for 2030 but changes radically by 2060. *PLoS One* **9**(3): e90662.

Sherwood, OA, Lehmann, MF, Schubert, CJ, Scott, DB, McCarthy, MD. 2011. Nutrient regime shift in the western North Atlantic indicated by compound-specific delta N-15 of deep-sea gorgonian corals. *Proceedings of the National Academy of Sciences of the United States of America* **108**: 1011–1015.

Siedlecki, SA, Salisbury, J, Gledhill, DK, Bastidas, C, Meseck, S, McGarry, K, Hunt, CW, Alexander, M, Lavoie, D, Wang, ZA, Scott, J. 2021. Projecting ocean acidification impacts for the Gulf of Maine to 2050: New tools and expectations. *Elementa: Science of the Anthropocene* 9(1): 00062. DOI: http://dx.doi.org/10.1525/elementa.2020.00062.

Smith, BE, Link, JS. 2010. The trophic dynamics of 50 finfish and 2 squid species on the Northeast US Continental Shelf. NOAA Technical Memorandum NMFS-NE-216. Woods Hole, MA: NOAA Northeast Fisheries Science Center.

Smith, LA, Link, JS, Cadrin, SX, Palka, DL. 2015. Consumption by marine mammals on the Northeast US continental shelf. *Ecological Applications* **25**: 373–389.

Sorte, CJB, Davidson, VE, Franklin, MC, Benes, KM, Doellman, MM, Etter, RJ, Hannigan, RE, Lubchenco, J, Menge, BA. 2017. Long-term declines in an intertidal foundation species parallel shifts in community composition. *Global change biology* **23**: 341–352.

Speirs, DC, Gurney, WSC, Heath, MR, Horbelt, W, Wood, SN, de Cuevas, BA. 2006. Ocean-scale modelling of the distribution, abundance, and seasonal dynamics of the copepod *Calanus finmarchicus*. *Marine Ecology Progress Series* **313**: 173–192.

Staudinger, MD. 2006. Seasonal and size-based predation on two species of squid by four fish predators on the Northwest Atlantic continental shelf. *Fishery Bulletin* **104** (4): 605–615.

Staudinger, MD, Goyert, H, Suca, JJ, Coleman, K, Welch, L, Llopiz, JK, Wiley, D, Altman, I, Applegate, A, Auster, P, Baumann, H. 2020. The role of sand lances (*Ammodytes* spp.) in the Northwest Atlantic Ecosystem: A synthesis of current knowledge with implications for conservation and management. *Fish and Fisheries* **21**(3): 522–556.

Staudinger, MD, Juanes, F. 2010. Size-dependent susceptibility of longfin inshore squid (*Loligo pealeii*) to attack and capture by two predators. *Journal of Experimental Marine Biology and Ecology* **393**: 106–113. DOI: http://dx.doi.org/10.1016/j.jembe.2010.07.005.

Staudinger, MD, Lynch, AJ, Gaichas, S, Fox, M, Gibson-Reinemer, D, Langan, JA, Teffer, AK, Thackeray, SJ, Winfield, IJ. 2021. How does climate change affect emergent properties of aquatic ecosystems? *Fisheries*. DOI: http://dx.doi.org/10.1002/FSH.10606.

Staudinger, MD, McAlarney, R, Pabst, A, McLellan, W. 2014. Foraging ecology and niche overlap in pygmy (*Kogia breviceps*) and dwarf (*Kogia sima*) sperm whales from waters of the U.S. mid-Atlantic coast. *Marine Mammal Science* **30**(2): 626–655. DOI: http://dx.doi.org/10.1111/mms.12064.

Staudinger, MD, Mills, KE, Stamieszkin, K, Record, NR, Hudak, CA, Allyn, A, Diamond, A, Friedland, KD, Golet, W, Henderson, ME, Hernandez, CM. 2019. It's about time: A synthesis of changing phenology in the Gulf of Maine ecosystem. *Fish Ocean* **28**(5): 532–566.

Steneck, RS, Wahle, RA. 2013. American lobster dynamics in a brave new ocean. *Canadian Journal of Fisheries and Aquatic Sciences* **70**: 1612–1624.

Stoll, JS, Fuller, E, Crona, BI. 2017. Uneven adaptive capacity among fishers in a sea of change. *PLoS One* **12**: e0178266.

Stortini, CH, Shackell, NL, Tyedmers, P, Beazley, K. 2015. Assessing marine species vulnerability to projected warming on the Scotian Shelf, Canada. *ICES Journal of Marine Science* **72**: 1731–1743.

Tanaka, K, Chen, Y. 2016. Modeling spatiotemporal variability of the bioclimate envelope of *Homarus americanus* in the coastal waters of Maine and New Hampshire. *Fisheries Research* **177**: 137–152.

Tanaka, KR, Chang, J-H, Xue, Y, Li, Z, Jacobson, LD, Chen, Y. 2018. Mesoscale climatic impacts on the distribution of *Homarus americanus* in the US inshore Gulf of Maine. *Canadian Journal of Fisheries and Aquatic Sciences*. DOI: http://dx.doi.org/10.1139/cjfas-2018-0075.

Tanaka, KR, Torre, MP, Saba, VS, Stock, CA, Chen, Y. 2020. An ensemble high-resolution projection of changes in the future habitat of American lobster and sea scallop in the Northeast US continental shelf. *Diversity and Distributions* **26**(8): 987–1001.

Taylor, KE, Stouffer, RJ, Meehl, GA. 2012. An overview of CMIP5 and the experiment design. *Bulletin of the American Meteorological Society* **93**: 485–498.

Teffer, AK, Staudinger, MD, Juanes, F. 2015. Trophic niche overlap among dolphinfish and co-occurring tunas near the northern edge of their range in the western North Atlantic. *Marine Biology* **162**(9): 1823–1840.

Thomas, AC, Pershing, AJ, Friedland, KD, Nye, JA, Mills, KE, Alexander, MA, Record, NR, Weatherbee, R, Henderson, ME, Drinkwater, K. 2017. Seasonal trends and phenology shifts in sea surface temperature on the North American northeastern continental shelf. *Elementa: Science of Anthropocene* **5**: 48.

Thorson, JT, Monnahan, CC, Cope, JM. 2015. The potential impact of time-variation in vital rates on fisheries management targets for marine fishes. *Fisheries Research* **169**: 8–17.

Townsend, DW. 1991. Influences of oceanographic processes on the biological productivity of the Gulf of Maine. *Reviews in Aquatic Sciences* **5**: 211–230.

Townsend, DW, Pettigrew, NR, Thomas, MA, Neary, MG, McGillicuddy, DJ, O'Donnell, J. 2015. Water masses and nutrient sources to the Gulf of Maine. *Journal of Marine Research* **73**: 93–122.

van der Kooij, J, Engelhard, GH, Righton, DA. 2016. Climate change and squid range expansion in the North Sea. *Journal of Biogeography* **43**(11): 2285–2298.

VanderZwaag, DL, Bailey, M, Shackell, NL. 2017. Canada–US fisheries management in the Gulf of Maine: Taking stock and charting future coordinates in the face of climate change. *Ocean Yearbook Online* **31**: 1–26.

Wahle, RA, Dellinger, L, Olszewski, S, Jekielek, P. 2015. American lobster nurseries of southern New England receding in the face of climate change. *ICES Journal of Marine Science* **72**: 69–78.

Wahle, RA, Gibson, M, Fogarty, M. 2009. Distinguishing disease impacts from larval supply effects in a lobster fishery collapse. *Marine Ecology Progress Series* **376**: 185–192.

Walsh, HJ, Richardson, DE, Marancik, KE, Hare, JA. 2015. Long-term changes in the distributions of larval and adult fish in the northeast US shelf ecosystem. *PLoS One* **10**(9): e0137382.

Weiskopf, SR, Rubenstein, MA, Crozier, LG, Gaichas, S, Griffis, R, Halofsky, JE, Hyde, KJ, Morelli, TL, Morisette, JT, Muñoz, RC, Pershing, AJ. 2020. Climate change effects on biodiversity, ecosystems, ecosystem services, and natural resource management in the United States. *Science of the Total Environment* **733**: 137782. DOI: http://dx.doi.org/10.1016/j.scitotenv.2020.137782.

Welch, WR. 1969. Changes in abundance of the green crab, *Carcinus maenas* in relation to recent temperature changes. *Fishery Bulletin* **67**: 337–345.

Whidden, SE. 2016. Patterns of natal recruitment in the Atlantic Puffin (*Fratercula arctica*) [Master's thesis]. Fredericton, Canada: University of New Brunswick.

Whitlow, WL. 2010. Changes in survivorship, behavior, and morphology in native soft-shell clams induced by invasive green crab predators. *Marine Ecology* **31**(3): 418–430.

Wilson, RJ, Banas, NS, Heath, MR, Speirs, DC. 2016. Projected impacts of 21st century climate change on diapause in *Calanus finmarchicus*. *Global Change Biology* **22**: 3332–3340.

Wing, B, Mercer, R. 1990. Temporary northern range extension of the squid *Loligo opalescens* in southeast Alaska. *The Veliger* **33**: 238–240.

Yakola, K. 2019. An examination of tern diets in a changing Gulf of Maine [Master's thesis]. Amherst, MA: University of Massachusetts Amherst.

Zeidberg, LD, Robison, BH. 2007. Invasive range expansion by the Humboldt squid, *Dosidicus gigas*, in the eastern North Pacific. *Proceedings of the National Academy of Sciences of the United States of America* **104**: 12946–12948.

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