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Several studies have documented fish populations changing in response to long-term warming. Over the last decade, sea surface temperatures in the Gulf of Maine increased faster than 99% of the global ocean. The warming, which was related to a northward shift in the Gulf Stream and to changes in the Atlantic Multidecadal and Pacific Decadal Oscillations, led to reduced recruitment and increased mortality in the region's Atlantic cod (*Gadus morhua*) stock. Failure to recognize the impact of warming on cod contributed to overfishing. Recovery of this fishery depends on sound management, but the size of the stock depends on future temperature conditions. The experience in the Gulf of Maine highlights the need to incorporate environmental factors into resource management.

Climate change is reshaping ecosystems in ways that impact resources and ecosystem services (*1*). Fisheries, with their tight coupling between ecosystem state and economic productivity, are a prime example of interacting social-ecological systems. The social and ecological value of a fishery depends first and foremost on the biomass of fish, and fishing has often been the dominant driver of the status of the resource and the economics of the fishing community. Modern fisheries management is designed to reduce harvesting levels in response to low stock biomass (and vice versa), creating a negative feedback that, in theory, will maintain steady long-term productivity (*2*).

A failure to detect changes in the environment or to act appropriately when changes are detected can jeopardize social-ecological systems (*3*). As climate change brings conditions that are increasingly outside the envelope of past experiences, the risks increase. The Gulf of Maine has warmed steadily, and the record warm conditions in 2012 impacted the fishery for American lobster (*4*). Here, we consider how ocean warming factored into the rapid decline of the Gulf of Maine cod stock (*5*).

We used sea surface temperature data to characterize temperature trends in the Gulf of Maine since 1982 and over the last decade (2004-2013). We compared the changes in this region with trends around the globe and related temperature variability to an index of Gulf Stream position and the Pacific Decadal Oscillation and the Atlantic Multidecadal Oscillation. We then examined the impact of temperature conditions in the Gulf of Maine on the recruitment and survival of Atlantic cod. The resulting temperature-dependent population dynamics model was used to project the rebuilding potential of this stock under future temperature scenarios.

From 1982-2013, daily satellite-derived sea surface temperature in the Gulf of Maine rose at a rate of 0.03°C yr^{-1} (R^2 = 0.12, p < 0.01, n = 11,688; Fig. 1A). This rate is higher than the global mean rate of 0.01°C yr^{-1} and led to gradual shifts in the distribution and abundance of fish populations (*6*–*8*). Beginning in 2004, the warming rate in the Gulf of Maine increased more than seven-fold to 0.23°C yr^{-1} (R^2 = 0.42, p < 0.01, n = 3,653). This period began with relatively cold conditions in 2004 and concluded with the two warmest years in the time series. The peak temperature in 2012 was part of a large "ocean heat wave" in the northwest Atlantic that persisted for nearly 18 months (*4*).

The recent 10 year warming trend is remarkable, even for a highly-variable part of the ocean like the northwest Atlantic. Over this period, substantial warming also occurred off of western Australia, in the western Pacific, and in the Barents Sea; and cooling was observed in the eastern Pacific and Bering Sea (Fig. 1B). The global ocean has a total area of 3.6 x 10^8 km^2, yet only 3.1 x 10^5 km^2 of the global ocean had warming rates greater than that in the Gulf of Maine over this time period. Thus, the Gulf of Maine has warmed faster than 99.9% of the global ocean between 2004 and 2013 (Fig. 1C). Using sea surface temperatures from 1900-2013, the likelihood of any 2° by 2° segment of the ocean exceeding this 10-year warming rate is less than 0.3%. Based on this analysis, the Gulf of Maine experienced decadal warming that few marine ecosystems have encountered.

As a first step toward diagnosing the potential drivers of the recent warming trend, we correlated the quarterly temperatures in the Gulf of Maine with large-scale climate indicators (table S1). An index of Gulf Stream position (*9*) has the strongest and most consistent relationship with Gulf of Maine temperatures. The correlations with the Gulf Stream Index (GSI) are positive and significant in all quarters, with the strongest correlation occurring in summer (r = 0.63, $p < 0.01$, n = 31). The Pacific Decadal Oscillation (PDO) (*10*) is negatively correlated with the Gulf of Maine temperatures during spring (r = −0.50) and summer (r = −0.67). Summer temperatures are also positively correlated with the Atlantic Multidecadal Oscillation (AMO) (*11*) (r = 0.48, $p < 0.01$, n = 31).

Building on the strong correlations with summer temperatures, we developed multiple regression models for summer Gulf of Maine temperatures using combinations of the three indices (Table 1). Based on AIC score, the best model used all three indices, and this model explained 70% of the variance in Gulf of Maine summer temperature (R^2 = 0.70, $p < 0.01$, AIC = 46.0, n = 31). This model was slightly better than one using GSI and the AMO (R^2 = 0.66, $p < 0.01$, AIC = 48.2, n = 31). We refit each model using data from 1982-2003, and then applied the model to the 2004-2012 period. The three-index and the GSI-AMO models had nearly identical out-of-sample performance, explaining 65% and 64% of the variance, respectively.

A long-term poleward shift in the Gulf Stream occurred over the 20th century and has been linked to increasing greenhouse gasses (*12*). Previous studies have reported an association between Gulf Stream position and temperatures in the northwest Atlantic (*7*, *13*), and an extreme northward shift in the Gulf Stream was documented during the record warm year of 2012 (*14*). Although the Gulf Stream does not directly enter the Gulf of Maine, northward shifts in the Gulf Stream are associated with reduced transport of cold waters southward on the continental shelf (*15*, *16*). The association between Gulf of Maine temperature and the PDO suggests an atmospheric component to the recent trend. A detailed heat-budget calculation for the 2012 event (*17*) found that the warming was due to increased heat flux associated with anomalously warm weather in 2011-2012. These results suggest that atmospheric teleconnections from the Pacific, changes in the circulation in the Atlantic Ocean, and background warming have contributed to the rapid warming in the Gulf of Maine.

The Gulf of Maine cod stock has been chronically overfished, prompting progressively stronger management, including the implementation of a quota-based management system in 2010. Despite these efforts, including a 73% cut in quotas in 2013, spawning stock biomass (*SSB*) continued to decline (Fig. 2A). The most recent assessment found that *SSB* in this stock is now less than 3,000 mt, only 4% of the spawning stock biomass that gives the maximum sustainable yield (SSB_{msy}) (*5*). This has prompted severe restrictions on the commercial cod fishery and the closure of the recreational fishery.

The Gulf of Maine is near the southern limit of cod, and previous studies have suggested that warming will lead to lower recruitment, suboptimal growth conditions, and reduced fishery productivity in the future (*18*–*20*). Using population estimates from the recent Gulf of Maine cod stock assessment (*5*), we fit a series of stock-recruit models with and without a temperature effect (table S2). The best models exhibited negative relationships between age-1 recruitment and summer temperatures (table S3). Gulf of Maine cod spawn in the winter and spring, so the link with summer temperatures suggests a decrease in the survival of late-stage larvae and settling juveniles. Although the relationship with temperature is statistically robust, the exact mechanism for this is uncertain but may include changes in prey availability and/or predator risk. For example, the abundance of some zooplankton taxa that are prey for larval cod has declined in the Gulf of Maine cod habitat (*21*). Warmer temperatures could cause juvenile cod to move away from their preferred shallow habitat into deeper water where risks of predation are higher (*22*).

We also looked for other signatures of temperature within the population dynamics of cod. We found a strong association between the mortality of age-4 fish and fall temperatures from the current year and the second year of life (Fig. 2B, R^2 = 0.57, $p < 0.01$, n = 21). Age 4 represents an energetic bottleneck for cod due to the onset of reproduction and reduced feeding efficiency as fish transition from benthic to pelagic prey (*23*). Elevated temperatures increase metabolic costs in cod (*24*), exacerbating the energetic challenges at this age. The average weight-at-age of cod in the Gulf of Maine region has been below the long-term mean since 2002 (*25*), and these poorly conditioned fish will have a lower probability of survival (*26*).

The age-4 mortality relationship improves significantly with the addition of temperatures from the second year of life (table S6). This suggests that a portion of the estimated age-4 mortality reflects mortality over the juvenile period that is not explicitly captured in the assessment. Temperature may directly influence mortality in younger fish through metabolic processes described above; however, we hypothesize that predation mortality may also be higher during warm years. Many important cod predators migrate into the Gulf of Maine or have feeding behaviors that are strongly seasonal. During a warm year, spring-like conditions occur earlier in the year, and fall-like conditions occur later. During the 2012 heat wave, the spring warming occurred 21 days ahead of schedule, and fall cooling was delayed by a comparable amount (*4*). This change in phenology could result in an increase in natural mortality of 44% on its own, without any increase in predator biomass (see supplementary text).

If fishing pressure had been effectively reduced, the population should have rebuilt more during the cool years and then declined less rapidly during the warming period. Instead, fishing mortality rates consistently exceeded target levels, even though fishermen did not exceed their quotas. The quota-setting process that is at the heart of fisheries management is highly sensitive to the number of fish aging into the fishery in each year. For Gulf of Maine cod, age classes 4 and 5 dominate the biomass of the stock and the catch (*5*). The temperature-mortality relationship in Fig. 2B means that during warm years, fewer fish are available for the fishery. Not accounting for this effect leads to quotas that are too high. The resulting fishing mortality rate was thus above the intended levels, contributing to overfishing even though catches were within prescribed limits. Socioeconomic pressures further compounded the overfishing. In order to minimize the impact of the quota cuts on fishing communities, the New England Fishery Management Council elected to defer most of the cuts indicated for 2012 and 2013 until the second half of 2013. The socioeconomic adjustment coupled with the two warmest years in the record led to fishing mortality rates that were far above the levels needed to rebuild this stock.

The impact of temperature on Gulf of Maine cod recruitment was known at the start of the warming period (*20*), and stock-recruitment model fit to data up to 2003 and incorporating temperature produces recruitment estimates (Fig. 2A, yellow diamonds) that are similar to the assessment time series. Ignoring the influence of temperature produces recruitment estimates that are on average 100% and up to 360% higher than if temperature is included (Fig. 2A, gray squares). Based on a simple population dynamics model that incorporates temperature, the spawning stock biomass that produces the maximum sustainable yield (SSB_{msy}) has been declining steadily since 2002 (Fig. 3) rather than remaining constant as currently assumed. The failure to consider temperature impacts on Gulf of Maine cod recruitment created unrealistic expectations for how large this stock can be and how quickly it can rebuild.

We estimated the potential for rebuilding the Gulf of Maine cod stock under three different temperature scenarios: a "cool" scenario that warms at a rate of 0.02° yr^{-1}, a "warm" scenario that warms at 0.03° yr^{-1}, the mean rate from climate model projections, and a "hot" scenario that follows the 0.07°C yr^{-1} trend present in the summer temperature time series. If fishing mortality is completely eliminated, populations in the cool and warm scenarios could rebuild to the temperature-dependent SSB_{msy} in 2025, slightly longer than the 10 year rebuilding timeline established by US law, and the hot scenario would reach its target one year later (Fig. 3). Allowing a small amount of fishing ($F = 0.1$) would delay rebuilding by three years in the cool and warm scenarios and 8 years in the hot. Note that estimating SSB_{msy} without temperature produces a management target that may soon be unachievable. By 2030, a rebuilt fishery could produce more than 5,000 tons yr^{-1} under the warm scenario, a catch rate close to the average for the fishery for the previous decade. Under the hot scenario, the fishery would be 1,800 tons yr^{-1}—small, but potentially valuable. Thus, how quickly this fishery rebuilds now depends arguably as much on temperature as it does on fishing. Future management of Gulf of Maine cod would benefit from a reevaluation of harvest control rules and thorough management strategy evaluation of the application of temperature-dependent reference points and projections such as these.

As climate change pushes species poleward and reduces the productivity of some stocks, resource managers will be increasingly faced with trade-offs between the persistence of a species or population and the economic value of a fishery. Navigating decisions in this context requires both accurate projections of ecosystem state and stronger guidance from society in the form of new policies. Social-ecological systems that depend on steady state or are slow to recognize and adapt to environmental change are unlikely to meet their ecological and economic goals in a rapidly changing world.

REFERENCES AND NOTES

1. E. J. Nelson, P. Kareiva, M. Ruckelshaus, K. Arkema, G. Geller, E. Girvetz, D. Goodrich, V. Matzek, M. Pinsky, W. Reid, M. Saunders, D. Semmens, H. Tallis, Climate change's impact on key ecosystem services and the human well-being they support in the US. *Front. Ecol. Environ.* **11**, 483–493 (2013). doi:10.1890/120312

2. R. Mahon, P. McConney, R. N. Roy, Governing fisheries as complex adaptive systems. *Mar. Policy* **32**, 104–112 (2008). doi:10.1016/j.marpol.2007.04.011

3. C. S. Holling, Understanding the complexity of economic, ecological, and social systems. *Ecosystems* **4**, 390–405 (2001). doi:10.1007/s10021-001-0101-5

4. K. E. Mills, A. Pershing, C. Brown, Y. Chen, F.-S. Chiang, D. Holland, S. Lehuta, J. Nye, J. Sun, A. Thomas, R. Wahle, Fisheries management in a changing climate: Lessons from the 2012 ocean heat wave. *Oceanography* **26**, 191–195 (2013). doi:10.5670/oceanog.2013.27

5. M. C. Palmer, *2014 Assessment Update Report of the Gulf of Maine Atlantic Cod Stock* (U.S. Department of Commerce, 2014).

6. J. A. Nye, J. S. Link, J. A. Hare, W. J. Overholtz, Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. *Mar. Ecol. Prog. Ser.* **393**, 111–129 (2009). doi:10.3354/meps08220

7. J. A. Nye, T. M. Joyce, Y.-O. Kwon, J. S. Link, Silver hake tracks changes in Northwest Atlantic circulation. *Nat. Commun.* **2**, 412 (2011). Medline doi:10.1038/ncomms1420

8. M. L. Pinsky, B. Worm, M. J. Fogarty, J. L. Sarmiento, S. A. Levin, Marine taxa track local climate velocities. *Science* **341**, 1239–1242 (2013). Medline

9. T. J. Joyce, C. Deser, M. A. Spall, The relation between decadal variability of Subtropical Mode Water and the North Atlantic Oscillation. *J. Clim.* **13**, 2550–

2569 (2000). doi:10.1175/1520-0442(2000)013<2550:TRBDVO>2.0.CO;2

10. N. J. Mantua, S. R. Hare, The Pacific Decadal Oscillation. *J. Oceanogr.* **58**, 35–44 (2002). doi:10.1023/A:1015820616384

11. R. A. Kerr, A North Atlantic climate pacemaker for the centuries. *Science* **288**, 1984–1985 (2000). Medline doi:10.1126/science.288.5473.1984

12. L. Wu, W. Cai, L. Zhang, H. Nakamura, A. Timmermann, T. Joyce, M. J. McPhaden, M. Alexander, B. Qiu, M. Visbeck, P. Chang, B. Giese, Enhanced warming over the global subtropical western boundary currents. *Nat. Clim. Change* **2**, 161–166 (2012). doi:10.1038/nclimate1353

13. D. G. Mountain, J. Kane, Major changes in the Georges Bank ecosystem, 1980s to the 1990s. *Mar. Ecol. Prog. Ser.* **398**, 81–91 (2010). doi:10.3354/meps08323

14. G. G. Gawarkiewicz, R. E. Todd, A. J. Plueddemann, M. Andres, J. P. Manning. Direct interaction between the Gulf Stream and the shelfbreak south of New England. *Sci. Rep.* **2**, 553 (2012). doi:10.1038/srep00553

15. T. Rossby, R. L. Benway, Slow variations in mean path of the Gulf Stream east of Cape Hatteras. *Geophys. Res. Lett.* **27**, 117–120 (2000). doi:10.1029/1999GL002356

16. A. J. Pershing, C. H. Greene, C. Hannah, D. Sameoto, E. Head, D. G. Mountain, J. W. Jossie, M. C. Benfield, P. C. Reid, T. G. Durbin, Oceanographic responses to climate in the Northwest Atlantic. *Oceanography* **14**, 76–82 (2001). doi:10.5670/oceanog.2001.25

17. K. Chen, G. G. Gawarkiewicz, S. J. Lentz, J. M. Bane, Diagnosing the warming of the Northeastern U.S. Coastal Ocean in 2012: A linkage between the atmospheric jet stream variability and ocean response. *J. Geophys. Res.* **119**, 218–227 (2014). doi:10.1002/2013JC009393

18. B. Planque, T. Frédou, Temperature and the recruitment of Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **56**, 2069–2077 (1999). doi:10.1139/f99-114

19. K. F. Drinkwater, The response of Atlantic cod (*Gadus morhua*) to future climate change. *ICES J. Mar. Sci.* **62**, 1327–1337 (2005). doi:10.1016/j.icesjms.2005.05.015

20. M. Fogarty, L. Incze, K. Hayhoe, D. Mountain, J. Manning, Potential climate change impacts on Atlantic cod (*Gadus morhua*) off the Northeastern United States. *Mitig. Adapt. Strategies Glob. Change* **13**, 453–466 (2008). doi:10.1007/s11027-007-9131-4

21. K. D. Friedland, J. Kane, J. A. Hare, R. G. Lough, P. S. Fratantoni, M. J. Fogarty, J. A. Nye, Thermal habitat constraints on zooplankton species associated with Atlantic cod (*Gadus morhua*) on the US Northeast Continental Shelf. *Prog. Oceanogr.* **116**, 1–13 (2013). doi:10.1016/j.pocean.2013.05.011

22. J. E. Linehan, R. S. Gregory, D. C. Schneider, Predation risk of age-0 cod (*Gadus*) relative to depth and substrate in coastal waters. *J. Exp. Biol. Ecol.* **263**, 25–44 (2001). doi:10.1016/S0022-0981(01)00287-8

23. G. D. Sherwood, R. M. Rideout, S. B. Fudge, G. A. Rose, Influence of diet on growth, condition and reproductive capacity in Newfoundland and Labrador cod (*Gadus morhua*): Insights from stable carbon isotopes ($\delta^{13}C$). *Deep Sea Res. II* **54**, 2794–2809 (2007). doi:10.1016/j.dsr2.2007.08.007

24. C. Deutsch, A. Ferrel, B. Seibel, H.-O. Pörtner, R. B. Huey, Climate change tightens a metabolic constraint on marine habitats. *Science* **348**, 1132–1135 (2015). Medline doi:10.1126/science.aaa1605

25. Northeast Fisheries Science Center, *55th Northeast Regional Stock Assessment Workshop (55th SAW) Assessment Report* (U.S. Department of Commerce, 2013).

26. J. D. Dutil, Y. Lambert, Natural mortality from poor condition in Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **57**, 826–836 (2000). doi:10.1139/f00-023

27. R. W. Reynolds, T. M. Smith, C. Liu, D. B. Chelton, K. S. Casey, M. G. Schlax, Daily high-resolution-blended analyses for sea surface temperature. *J. Clim.* **20**, 5473–5496 (2007). doi:10.1175/2007JCLI1824.1

28. B. J. Pyper, R. M. Peterman, Comparison of methods to account for autocorrelation in correlation analyses of fish data. *Can. J. Fish. Aquat. Sci.* **55**, 2127–2140 (1998). doi:10.1139/f98-104

29. J. W. Hurrell, Decadal trends in the North Atlantic Oscillation: Regional temperatures and precipitation. *Science* **269**, 676–679 (1995). Medline doi:10.1126/science.269.5224.676

30. E. P. Ames, Atlantic cod stock structure in the Gulf of Maine. *Fisheries* **29**, 10–28 (2004). doi:10.1577/1548-8446(2004)29[10:ACSSIT]2.0.CO;2

31. A. I. Kovach, T. S. Breton, D. L. Berlinsky, L. Maceda, I. Wirgin, Fine-scale spatial and temporal genetic structure of Atlantic cod off the Atlantic coast of the USA. *Mar. Ecol. Prog. Ser.* **410**, 177–195 (2010). doi:10.3354/meps08612

32. L. A. Kerr, S. X. Cadrin, A. I. Kovach, Consequences of a mismatch between biological and management units on our perception of Atlantic cod off New England. *ICES J. Mar. Sci.* **71**, 1366–1381 (2014). doi:10.1093/icesjms/fsu113

33. S. M. L. Tallack, Regional growth estimates of Atlantic cod, *Gadus morhua*: Applications of the maximum likelihood GROTAG model to tagging data in the Gulf of Maine (USA/Canada) region. *Fish. Res.* **99**, 137–150 (2009). doi:10.1016/j.fishres.2009.05.014

34. K. E. Taylor, R. J. Stouffer, G. A. Meehl, An Overview of CMIP5 and the experiment design. *Bull. Am. Meterol. Soc.* **93**, 485–498 (2012). doi:10.1175/BAMS-D-11-00094.1

35. K. E. Alexander, W. B. Leavenworth, J. Cournane, A. B. Cooper, S. Claesson, S. Brennan, G. Smith, L. Rains, K. Magness, R. Dunn, T. K. Law, R. Gee, W. Jeffrey Bolster, A. A. Rosenberg, Gulf of Maine cod in 1861: Historical analysis of fishery logbooks, with ecosystem implications. *Fish Fish.* **10**, 428–449 (2009). doi:10.1111/j.1467-2979.2009.00334.x

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SUPPLEMENTARY MATERIALS

www.sciencemag.org/cgi/content/full/science.aac9819/DC1
Materials and Methods
Figs. S1 to S6
Tables S1 to S5
References (*27*–*35*)

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Table 1. Linear models relating Gulf of Maine summer temperature to climate indicators. GSI = Gulf Stream Index, PDO = Pacific Decadal Oscillation Index, AMO = Atlantic Multidecadal Oscillation Index. The final model uses all three indices. The first set of statistics refer to the models fit to the entire 1982-2013 record. The models were also fit to the 1982-2003 period then projected on to the 2004-2013 period. The last two columns summarize the out of sample performance of the models.

Time series 1	Time series 2	1982-2013			2004-2013 Out of Sample	
		R^2	p	AIC	r^2	p
GSI	—	0.39	0.00	63.92	0.50	0.00
	PDO	0.58	0.00	54.41	0.54	0.00
	AMO	0.66	0.00	48.15	0.64	0.00
PDO	—	0.45	0.00	60.77	0.28	0.01
	AMO	0.50	0.00	59.78	0.32	0.01
AMO	—	0.23	0.01	71.06	0.11	0.13
All		0.70	0.00	45.99	0.65	0.00

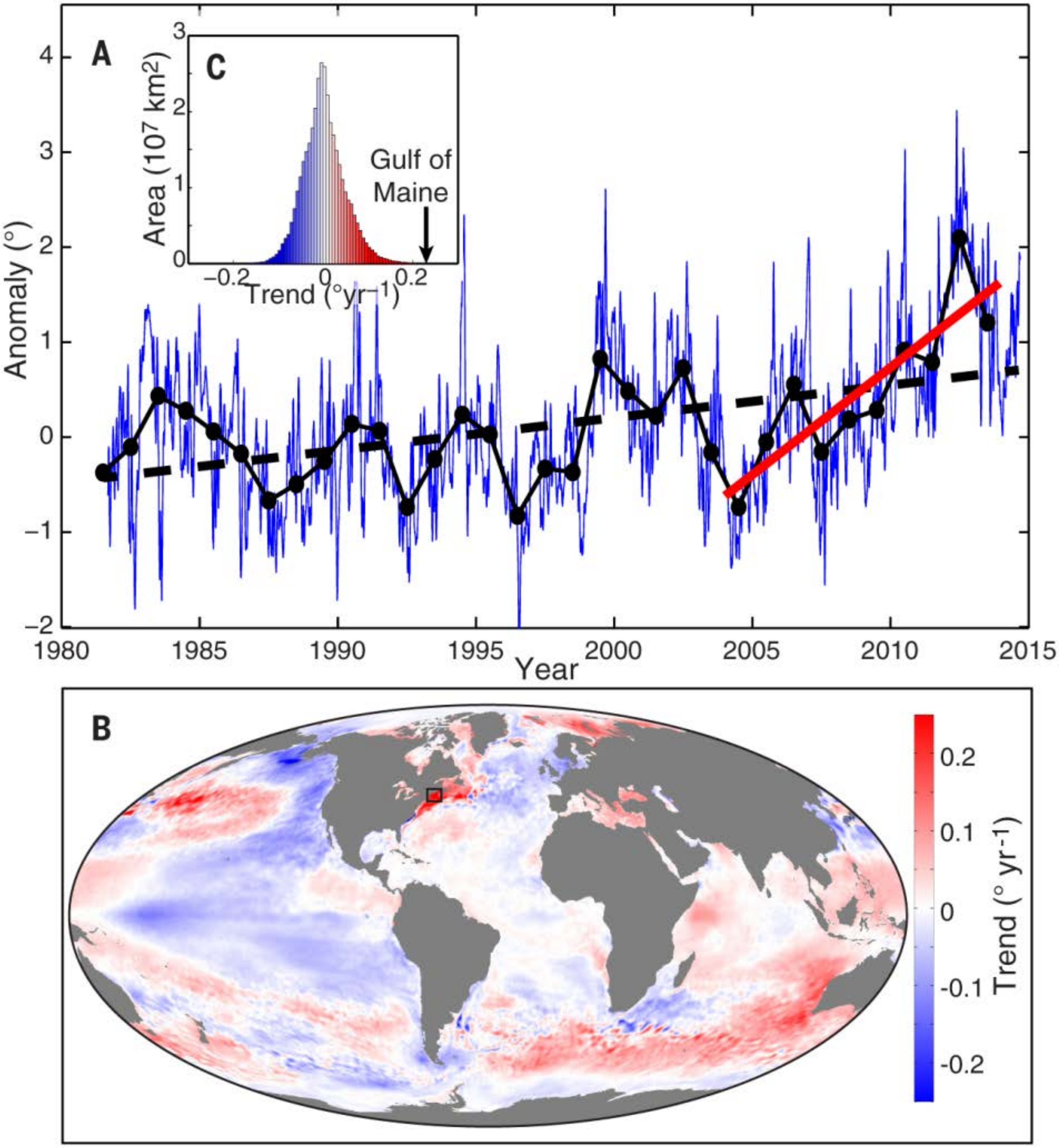

Fig. 1. Sea surface temperature trends from the Gulf of Maine and the global ocean. (**A**) Daily (blue, 15d smoothed) and annual (black dots) SST anomalies from 1982-2013 with the long-term trend (black dashed line) and trend over the last decade (2004-2013) (red solid line). (**B**) Global SST trends (° yr^{-1}) over the period 2004-2013. The Gulf of Maine is outlined in black. (**C**) Histogram of global 2004-2013 SST trends with the trend from the Gulf of Maine indicated at the right extreme of distribution.

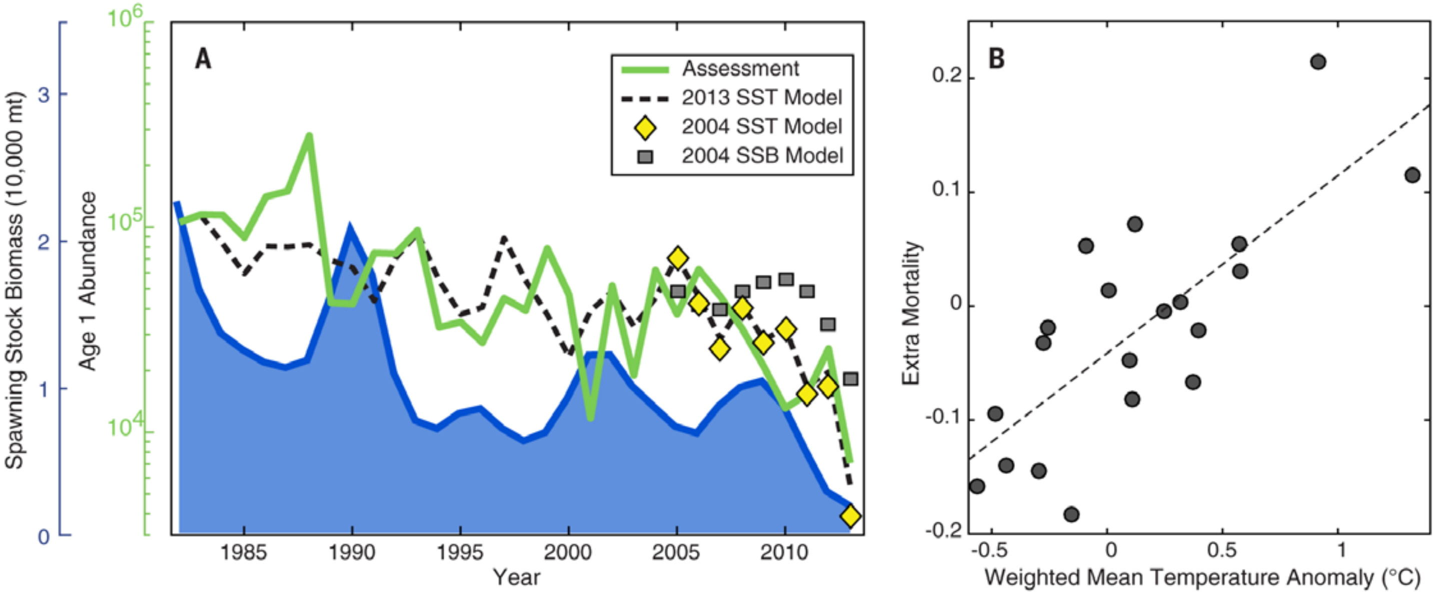

Fig. 2. Relationships between Gulf of Maine cod and temperature. (**A**) Time series of Gulf of Maine cod spawning stock biomass (blue), and age-1 recruitment (green) from the 2014 assessment. Cod age-1 recruitment modeled using adult biomass and summer temperatures (dashed line). The gray squares are recruitment estimated using a model without a temperature effect fit to data prior to 2004. The yellow diamonds are a temperature-dependent model fit to this earlier period. (**B**) Mortality of age-4 cod as a function of temperature ($R^2 = 0.57$, $p < 0.01$, $n = 21$). The temperature is composed of the fall values from the current year and three years prior, weighted using the coefficients from the linear model.

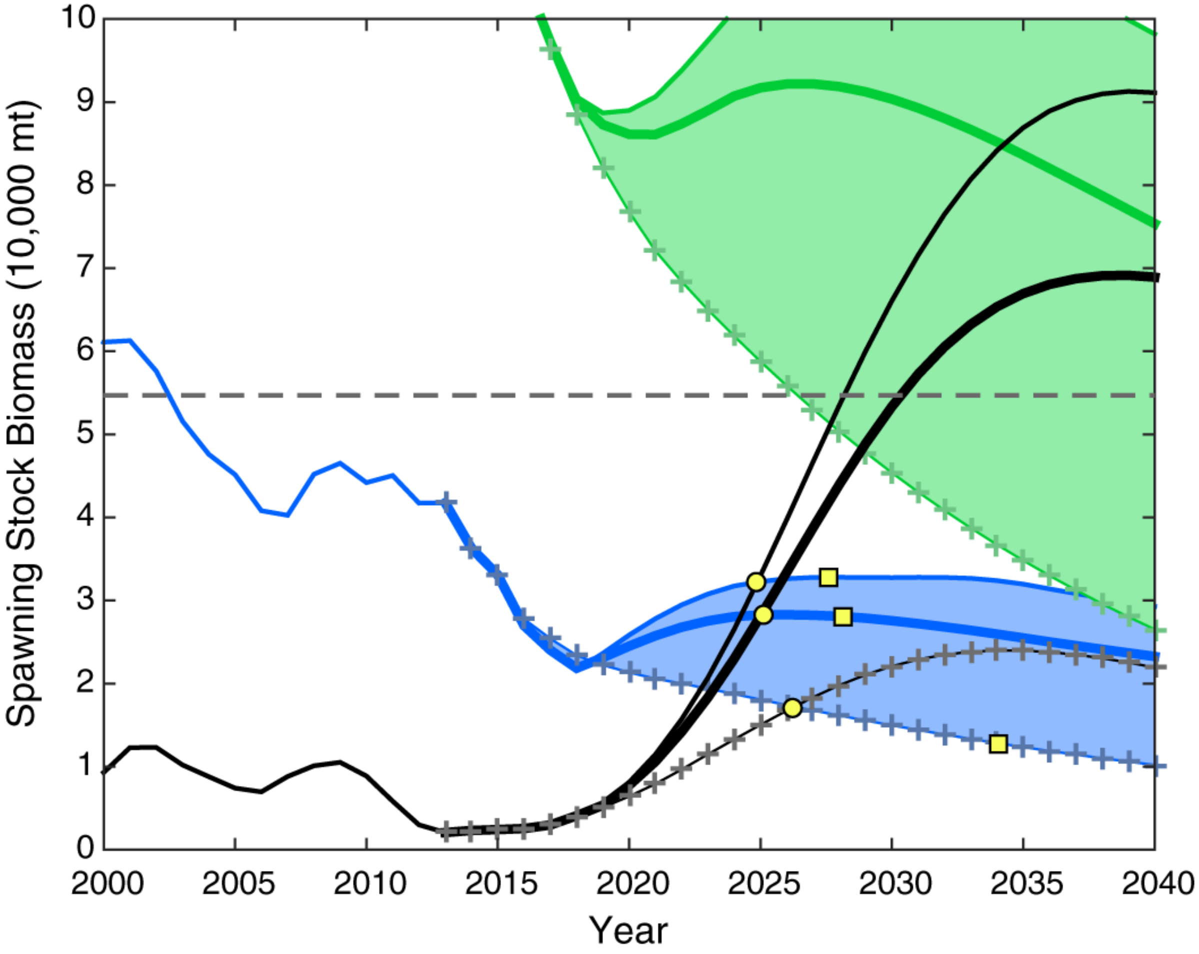

Fig. 3. Temperature-dependent rebuilding potential of Gulf of Maine cod. We simulated a population growing from the 2013 biomass (black curves) without fishing under three temperature scenarios: a cool scenario (solid line) represented by the 10% lower bound of the CMIP-5 ensemble, a warm scenario (heavy line) represented by the climate model ensemble mean, and a hot scenario ("+"s) with warming at the 0.07° yr^{-1} rate observed in the summer in the Gulf of Maine since 1982. This population is contrasted against an estimate of the temperature-dependent SSB_{msy} (blue lines and shading), an estimate of SSB_{msy} without accounting for temperature (grey dashed line), and the carrying capacity of the population (green lines and shading). The yellow circles mark where the rebuilding population reaches the temperature-dependent SSB_{msy}, squares denote when a population fished at $F = 0.1$ would be rebuilt.