FISHERIES

Impacts of historical warming on marine fisheries production

Christopher M. Free[1,2]*, James T. Thorson[3,4], Malin L. Pinsky[5], Kiva L. Oken[1,6], John Wiedenmann[5], Olaf P. Jensen[1]

Climate change is altering habitats for marine fishes and invertebrates, but the net effect of these changes on potential food production is unknown. We used temperature-dependent population models to measure the influence of warming on the productivity of 235 populations of 124 species in 38 ecoregions. Some populations responded significantly positively (n = 9 populations) and others responded significantly negatively (n = 19 populations) to warming, with the direction and magnitude of the response explained by ecoregion, taxonomy, life history, and exploitation history. Hindcasts indicate that the maximum sustainable yield of the evaluated populations decreased by 4.1% from 1930 to 2010, with five ecoregions experiencing losses of 15 to 35%. Outcomes of fisheries management—including long-term food provisioning—will be improved by accounting for changing productivity in a warmer ocean.

Marine fishes and invertebrates have become an increasingly important source of food as the human population has grown, especially in coastal, developing countries, where they provide as much as 50% of animal protein consumption (*1*, *2*). However, ocean warming is driving changes in ocean circulation and stratification (*3*), losses in oxygen concentration (*4*), and shifts in primary productivity (*5*). As a result, marine fish populations are experiencing large-scale redistributions (*6*), increased physiological stress (*7*), and altered food availability (*8*). Understanding the net effect of these changes on fisheries productivity (i.e., the net population increase at a given biomass) is crucial to identifying the level of biomass that will optimize fisheries outcomes, including long-term food provisioning. Appropriately identifying a target level of population biomass is in turn important for fisheries managers trying to regulate human impacts (e.g., through catch and effort restrictions) to achieve fisheries targets.

Although the question of future fisheries productivity under climate change has received extensive attention (*9*–*12*), the ocean has already warmed considerably (*13*), and the impacts of this warming may have already affected global marine fisheries productivity. Retrospective analyses of historical temperature and population dynamics are especially important for quantifying the magnitude of historical climate effects, testing hypotheses, and understanding variation among regions (*14*). A promising approach is to measure the impact of historical warming on the production of biomass and the maximum catch that can be repeatedly harvested from that biomass, a quantity termed the maximum sustainable yield (MSY). Although sometimes criticized (*15*), MSY is the catch limit for the U.N. Convention on the Law of Sea, U.N. Sustainable Development Goal 14, and many other fisheries agreements because it maximizes long-term food provisioning potential from the ocean.

Simple correlations of fisheries production and climate indices often fail because effects are nonlinear and depend on interactions between multiple processes (*8*, *16*). In this study, we instead used a mechanistic population dynamics model (*17*) to measure the effects of ocean temperature (*18*) on the productivity of 235 global fish and invertebrate populations (*19*). The analyzed populations represent 124 species, 38 ecoregions, and ~33% of reported global catch. We then used the model to hindcast temperature-driven changes in MSY from 1930 to 2010 (*20*).

We estimated the influence of temperature on productivity as a random effect, where temperature influences for each population were informed by a normal distribution representing the effect of temperature across all populations. The most parsimonious model, as identified by Akaike's information criterion (*21*), structured the temperature influence by marine ecoregion (table S1). The mean of the random effects distribution for the influence of temperature was not significantly different from zero (Fig. 1A), indicating that populations benefiting from ocean warming were roughly offset in number and magnitude by those that were negatively impacted. However, the productivities of 28 populations (12%) were either significantly negatively (n = 19 populations; 8%) or significantly positively (n = 9 populations; 4%) influenced by warming (Fig. 1A and table S2). By comparing with a null model (Fig. 1B), we found stronger temperature influences than would be expected by chance (P < 0.001; binomial exact test). The estimation of temperature influences was also robust to a number of other assumptions regarding input data and model structure (figs. S1 to S15 and supplementary text).

The importance of marine ecoregion in structuring temperature influence suggests that the impact of warming on ecosystem structure and dynamics manifests similarly for populations inhabiting the same region (*22*). For example, we found negative mean temperature influences in the Celtic-Biscay Shelf and North Sea ecoregions (figs. S16 and S17), where warming has enhanced stratification and driven shifts in primary productivity, with cascading effects on zooplankton (*23*), forage fish (*24*), and groundfish productivity (*25*). In the neighboring Baltic Sea, we found a positive mean temperature influence, where cooler water temperatures delay and reduce spring zooplankton production and result in reduced survival of larval fish (*26*, *27*).

Taxonomic family was also an important, though somewhat weaker, driver of temperature influence, consistent with the phylogenetic conservation of life history traits and vulnerabilities (*28*). The commercially important gadid family (codfishes) and ecologically important ammodytid family (sand eels) both exhibited negative mean temperature effects (fig. S17). Populations of species in both families are concentrated in the North Atlantic (26 of 36 gadid populations and all three sand eel populations) and will be especially susceptible to the continued rapid warming predicted for this region (*29*).

The influence of temperature on fisheries productivity was also well explained by species traits and population characteristics (table S3). For example, the position of a population within its species-specific thermal niche determined the influence of warming: Atlantic cod (*Gadus morhua*) and Atlantic herring (*Clupea harengus*) populations at the warm ends of their thermal niches were more vulnerable to warming than populations at the cool ends of their thermal niches (Fig. 2C). In fact, populations in cooler environments often benefited from historical warming, though such benefits may be expected to decline with further warming, consistent with thermal niche theory (*30*). We also found that fishes with faster life histories (e.g., faster growth, earlier age at maturity, and shorter life spans) were more responsive to warming, both positively and negatively, than fishes with slower life histories (Fig. 2B and fig. S19). Fast-growing species are also known to shift locations more rapidly (*6*, *31*), and geographic shifts in or out of a region may help drive productivity changes for these and other shifting species (*32*). Habitat, trophic level, body size, latitude, and population size did not substantially structure temperature influences (figs. S18 to S23).

We also found that exploitation history and temperature change interacted to determine the vulnerability of populations to warming. Populations that had experienced intense and prolonged overfishing were more likely to be negatively influenced by warming, especially when they had

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also experienced rapid warming (>0.2°C per decade) (Fig. 2A). This interaction likely arises through several mechanisms. First, fishing can truncate age distributions (*33*) and select for earlier maturation or reduced body sizes (*34*), both of which can decrease reproductive output (*35*). Fishing can also reduce intraspecific diversity, alter species interactions, and damage habitat (*36*). As a result, overfishing can magnify fluctuations in abundance due to environmental variability (*37*, *38*) and interact with life history and climate variability to increase the likelihood of population collapse (*39*). Thus, overfishing has reduced the resilience of populations to climate change, and climate change will likely hinder efforts to rebuild overfished populations (*40*).

We used the model estimates of temperature influence, intrinsic rate of increase, and carrying capacity along with historical temperature data to hindcast MSY from 1930 to 2010. We chose this time period to minimize extrapolation to temperatures cooler or warmer than those used in model fitting (figs. S24 and S25). We estimate that the combined MSY from the 235 populations decreased by 4.1% (1.4 million metric tons), from 35.2 million metric tons in 1930 to 1939 to 33.8 million metric tons in 2001 to 2010 (Fig. 3A). The 95% confidence interval for this trend ranged from a 9.0% decline to a 0.3% increase, indicating much stronger support for declining productivity

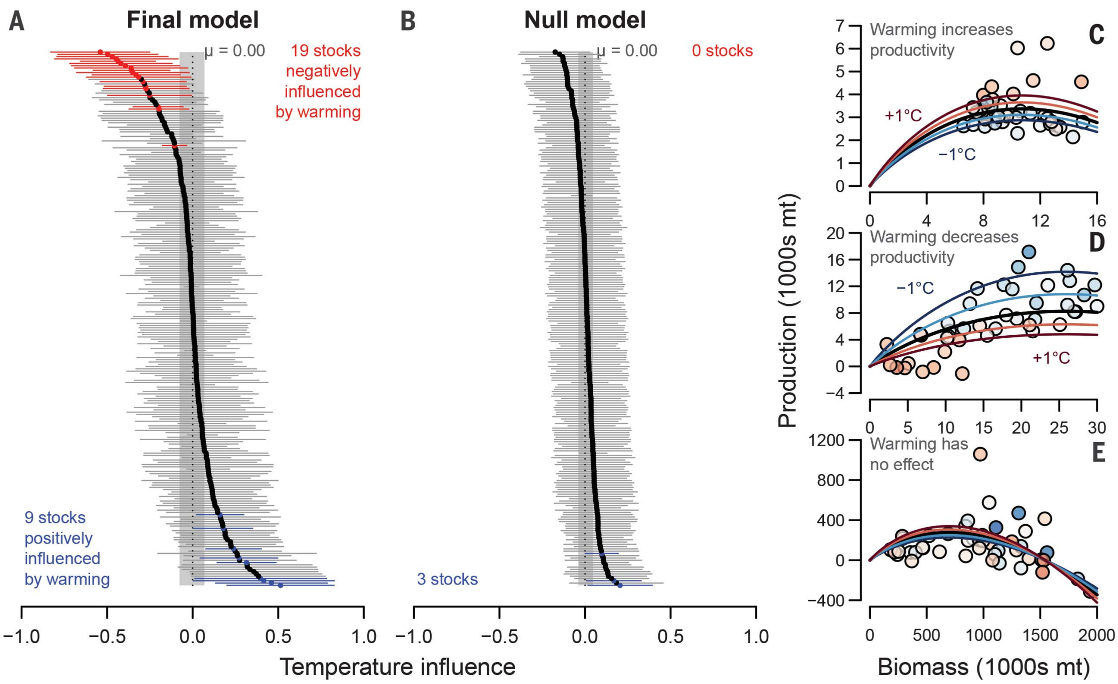

Fig. 1. Influence of warming on fisheries productivity. Distribution of temperature influences estimated by (**A**) the final model and (**B**) the null model. Examples of populations where historical ocean warming (**C**) increased productivity (black sea bass in the U.S. mid-Atlantic), (**D**) decreased productivity (Atlantic cod in the Irish Sea), and (**E**) did not affect productivity (Atlantic herring in the northwest Atlantic). In (A) and (B), points show mean estimates and error bars show 95% confidence intervals. Significant positive and negative temperature influences are shown in blue and red, respectively. The shaded gray column indicates the 95% confidence interval for the global mean (μ) of the temperature influences. The null model is fit to simulated temperature time series exhibiting the same means, variances, autoregressive properties, and trends as the original time series. In (C) through (E), blue and red points represent cooler- and warmer-than-average years, respectively. Black lines show production at the population's average temperature. Blue and red lines show production at temperatures progressively cooler and warmer than the average, respectively (−1.0°, −0.5°, +0.5°, and +1.0°C). mt, metric tons.

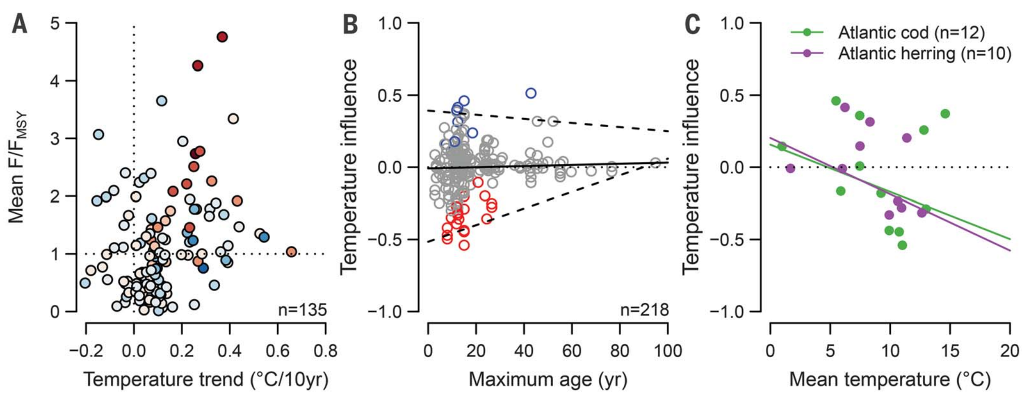

Fig. 2. Drivers of the influence of warming on fisheries productivity. (**A**) More and larger negative influences of warming for populations with histories of overfishing and rapid temperature increase. Points represent individual populations and are colored by the direction and magnitude of their temperature influence (deeper blue, more positive; deeper red, more negative). F/F_{MSY} is the ratio of fishing mortality (F) to the fishing mortality that produces MSY (F_{MSY}). Values greater than one indicate overfishing. (**B**) Larger and more significant influences of temperature for populations of species with faster life histories (i.e., shorter life spans). Points represent individual populations and are colored by significance (blue, positive; red, negative; gray, not significant). The solid line shows the 50th-percentile quantile regression fit, and dashed lines show the 2.5 and 97.5% quantile regression fits. (**C**) Increasingly negative influences for populations at the warm ends of their thermal niches for the two species with ≥10 populations. Lines show Theil-Sen regression fits. Theil-Sen regression, a form of robust regression, identifies the median slope of lines through all possible point pairs and is insensitive to outliers and end points in small datasets.

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during this period. Losses from populations responding negatively to warming outweighed gains from those responding positively because negatively responding populations constituted a larger biomass (Fig. 3, B and C). The greatest losses in productivity occurred in the Sea of Japan, North Sea, Iberian Coastal, Kuroshio Current, and Celtic-Biscay Shelf ecoregions, whereas the greatest gains occurred in the Labrador-Newfoundland, Baltic Sea, Indian Ocean, and Northeast U.S. Shelf ecoregions (Fig. 4 and table S4). The East Asian ecoregions experienced some of the largest warming-driven declines in MSY (8 to 34%) and support some of the largest and fastest-growing human populations in the world (*41*).

Our results present a new map of "winning" and "losing" ecosystems under ocean warming (Fig. 4). Studies that project fisheries productivity under future emissions scenarios often predict increases in productivity at the poles and decreases at the equator (*10*, *11*, *42*). We see no evidence for this prediction over the observed time period (Fig. 4 and figs. S16, S18, and S26), suggesting that contemporary range shifts have yet to drive productivity to the poles or that this prediction is driven by populations not evaluated in this work. Our estimates of ecoregion-scale trends in productivity were also uncorrelated with trends in recruitment potential (fig. S27) (*14*), suggesting that climate effects on the other components of productivity—somatic growth and natural mortality—may be strong enough to offset effects on recruitment. However, declines in North Sea fisheries productivity are consistent with studies showing declines in forage fish (*24*) and groundfish (*25*) productivity induced by ocean warming. Declines in East Asian fisheries productivity are consistent with single-species studies documenting negative climate impacts in the region (*43*), though community-scale studies suggest that declining predator productivity may be balanced by corresponding increases in prey productivity (*44*).

Our study is limited in three ways. First, we evaluated only the influence of temperature on productivity, though other factors such as changing primary production, dissolved oxygen, pH, and habitat availability may also be influential (*45*). Progress in the development of global historical datasets for environmental variables other than temperature would enable more comprehensive investigations in the future. Second, the fisheries database used in this study presents a nonrandom selection of global fish populations (*19*). By identifying traits that can explain vulnerability to warming, however, our analysis provides an approach for extrapolating to unevaluated populations. For example, we found that 162 fish populations (10.6%) in the much more complete Food and Agriculture Organization (FAO) landings database (*1*) exhibit the characteristics associated with a negative effect of warming on productivity—that is, they are overfished, have experienced warming, and are at the warm ends of their thermal niches (figs. S28 to S30). This proportion is comparable to the proportion of data-rich populations that have experienced a negative influence of historical warming (8%) (Fig. 1A). Region-specific studies are necessary to better understand the impacts of warming on important but poorly described fisheries, especially those of tropical developing nations. Lastly, the use of population model output as data has been criticized because of difficulties in accounting for model assumptions, uncertainty, and bias in post hoc analyses (*46*). We addressed these concerns by following best practices for stock assessment meta-analysis (*47*) and by explicitly confirming that the results were not influenced by the methods of the source population models (supplementary text).

A number of analytical constraints imply that the impacts of ocean warming on fisheries productivity may be more negative than we could detect. Data limitations required us to estimate a

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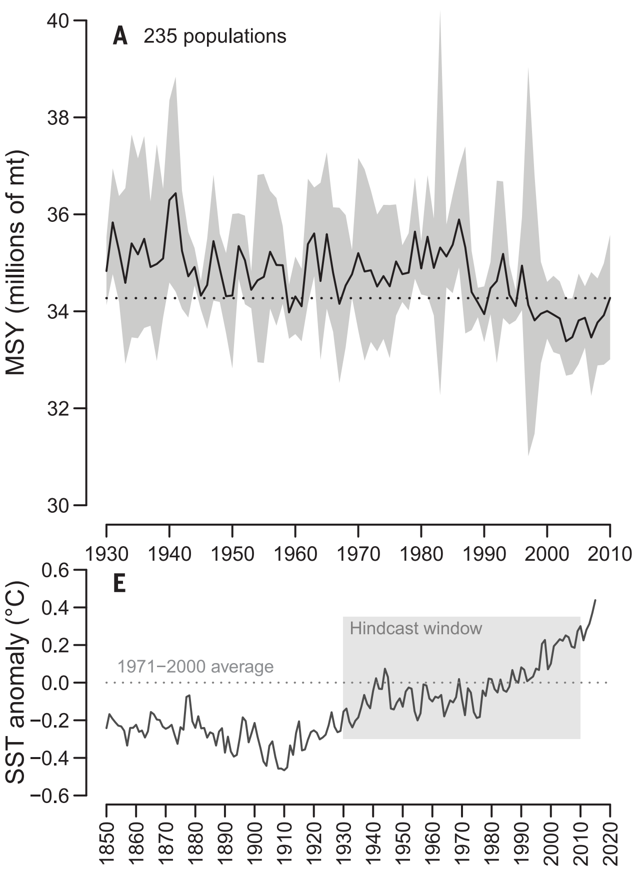

Fig. 3. Hindcast of temperature-dependent MSY. MSY hindcasts are shown (**A**) for all populations and for populations with (**B**) significant positive, (**C**) significant negative, and (**D**) nonsignificant influences of temperature on productivity. Solid lines indicate the median MSY estimates, shading indicates the 95% confidence intervals, and dashed lines show MSY at average temperature. mt, metric tons. (**E**) The mean global sea surface temperature (SST) anomaly from 1850 to 2015.

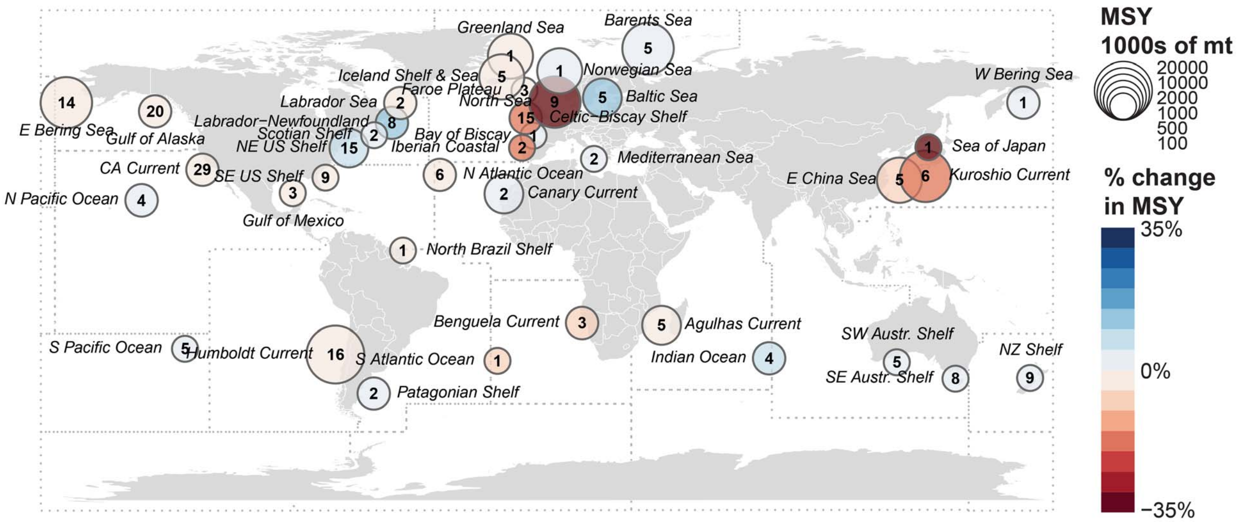

Fig. 4. Percent change in mean MSY between the period from 1930 to 1939 and the period from 2001 to 2010 by ecoregion. Points are scaled to the MSY at average temperature, and the number of populations in each ecoregion is shown inside the point. Dashed lines indicate FAO major fishing areas. Aust., Australian; NZ, New Zealand; mt, metric tons.

monotonic influence of warming on production (i.e., warming could only increase or decrease productivity for a given population). However, the aerobic performance of individual fish is dome shaped [it increases as temperatures warm toward some thermal optimum but decreases once temperatures exceed this optimum (*30*)] and is likely to remain dome shaped at the population scale through cumulative impacts on growth, mortality, and recruitment (*48*). Populations identified as responding positively to warming are thus unlikely to maintain productivity gains as continued warming (*13*, *49*) drives these populations past their thermal optima (see Atlantic cod and herring in Fig. 2C).

As the world's human population and demand for seafood have grown (*1*), ocean warming has driven declines in marine fisheries productivity and the potential for sustainable fisheries catches. Simultaneously, overfishing has compromised the resilience of many marine fish and invertebrate populations to climate change. However, prompt improvements in fisheries management could maintain fisheries yields and profits into the future (*32*). Thus, preventing overfishing and developing management strategies that are robust to temperature-driven changes in productivity are essential if society is to maintain and rebuild the capacity for global wild-capture fisheries to supply food and support livelihoods in a warming ocean.

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SUPPLEMENTARY MATERIALS

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Supplementary Text
Figs. S1 to S30
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Accounting for a warming ocean

Fisheries provide food and support livelihoods across the world. They are also under extreme pressure, with many stocks overfished and poorly managed. Climate change will add to the burden fish stocks bear, but such impacts remain largely unknown. Free *et al.* used temperature-specific models and hindcasting across fish stocks to determine the degree to which warming has, and will, affect fish species (see the Perspective by Plagányi). They found that an overall reduction in yield has occurred over the past 80 years. Furthermore, although some species are predicted to respond positively to warming waters, the majority will experience a negative impact on growth. As our world warms, responsible and active management of fisheries harvests will become even more important.

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