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CLIMATE CHANGE IMPACTS ON MISMATCHES BETWEEN PHYTOPLANKTON BLOOMS AND FISH SPAWNING PHENOLOGY

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Abstract

Substantial interannual variability in marine fish recruitment (*i.e.*, the number of young fish entering a fishery each year) has been hypothesized to be related to whether the timings of fish spawning matches that of seasonal plankton blooms. Environmental processes that control the phenology of blooms, such as stratification, may differ from those that influence fish spawning, such as temperature-linked reproductive maturation. These different controlling mechanisms could cause the timing of these events to diverge under climate change with negative consequences for fisheries. We use an earth system model to examine the impact of a high-emissions climate-warming scenario (RCP8.5) on the future spawning time of two classes of temperate, epipelagic fishes: "geographic spawners" whose spawning grounds are defined by fixed geographic features (*e.g.*, rivers, estuaries, reefs), and "environmental spawners" whose spawning grounds move responding to variations in environmental properties, such as temperature. By the century's end, our results indicate that projections of increased stratification cause spring and summer phytoplankton blooms start 16 days earlier on average (±0.05 days S.E.) at latitudes >40°N. The temperature-linked phenology of geographic spawners changes at a rate twice as fast as phytoplankton, causing these fishes to spawn before the bloom starts across >85% of this region. "Extreme events", defined here as seasonal mismatches >30 days that could lead to fish recruitment failure, increase 10-fold for geographic spawners in many areas under the RCP8.5 scenario. Mismatches between environmental spawners and phytoplankton were smaller and less widespread, although sizable mismatches still emerged in some regions. This indicates that range shifts undertaken by environmental spawners may increase the resiliency of fishes to climate change impacts associated with phenological mismatches, potentially buffering against declines in larval fish survival, recruitment, and fisheries. Our model results are supported by empirical evidence from ecosystems with multidecadal observations of both fish and phytoplankton phenology.

Introduction

The number of young fish entering a fishery each year (*i.e*., recruitment) can vary interannually by orders of magnitude (Hjort, 1926), resulting in sizable fluctuations in fisheries productivity and uncertainty in fisheries management. One hypothesis explaining recruitment variability is that mismatches between the seasonal timings of fish reproduction and the peak

biomass of larval fish prey (*i.e.*, medium-to-large zooplankton) can lead to high larval mortality due to starvation or increased predation on slower growing larvae (Cushing, 1990). Since multiple processes acting on early life history stages of fishes influence recruitment (Houde, 2008), a good match between fish spawning and zooplankton biomass does not necessarily guarantee high recruitment, but a poor match typically is associated with lower-than-average recruitment (Platt, Fuentes-Yaco, & Frank, 2003; Durant, Hjermann, Ottersen, & Stenseth, 2007). Larvae of many fish species often reach their first-feeding stage at approximately the same time that zooplankton biomass increases in response to the spring phytoplankton bloom. Consequently, phytoplankton bloom phenology has been linked to the productivity of fishes as diverse as haddock, herring, and salmon (Platt et al., 2003; Schweigert et al., 2013; Malick, Cox, Mueter, & Peterman, 2015).

At latitudes >40°N, a key control on spring phytoplankton blooms is light limitation on photosynthesis associated with low winter irradiance, vigorous mixing of phytoplankton below the well-lit euphotic layer and, in some cases, the presence of sea ice (Boyce, Petrie, Frank, Worm, & Leggett, 2017). The spring increase in light and stratification that reduces deep mixing and favors phytoplankton growth is affected by temperature and heat flux (Taylor & Ferrari, 2011), salinity (Song, Ji, Stock , & Wang, 2010), wind (Ueyama & Monger, 2005), and eddies (Mahadevan, D'Asaro, Lee, & Perry, 2012). Under climate change, stratification is projected to increase throughout most of the ocean (Capotondi, Alexander, Bond, Curchitser, & Scott, 2012), contributing to robust projections of earlier phytoplankton blooms in subpolar and polar regions across Earth System Models (ESMs) (Henson, Cole, Beaulieu, & Yool, 2013; Henson, Cole, Hopkins, Martin, & Yool, 2017). In contrast to phytoplankton, temperature and photoperiod are the predominant factors affecting fish phenology (Pankhurst & Porter, 2003). Temperature accelerates metabolism and controls the rate of gonadal development in poikilothermic fishes (Pankhurst & Porter, 2003; Neuheimer & Mackenzie, 2014). Consequently, temperature often has a direct, physiological impact on fish phenology, but is only one of several factors exerting indirect effects on phytoplankton phenology. We hypothesize that these differences in driving factors may increase the frequency of seasonal mismatches between trophic levels under climate change. This hypothesis is supported by a meta-analysis of recent changes in marine organismal phenology indicating larval fishes have undergone larger phenological shifts over the last several decades than have phytoplankton (Poloczanska et al., 2013). However, the sample size of larval

fish species included in the meta-analysis (*n*=2) is too small to determine if this pattern is pervasive.

To further assess the hypothesis of increased seasonal mismatches between trophic levels, we used an ESM to develop the first projections of phenological mismatches between fish spawning and phytoplankton blooms. We focused on phytoplankton rather than zooplankton phenology since modeled chlorophyll can be validated globally with satellites (Fig. S1) while <20 time series of zooplankton phenology exist (Mackas et al., 2012). Also, chlorophyll concentration is correlated with global variations in fisheries yield (Friedland et al., 2012) and recruitment capacity (Britten, Dowd, & Worm, 2016). We modeled two categories of epipelagic, spring-spawning fishes (Reglero et al., 2012) whose spawning grounds were either tied to fixed geographic features or tracked climate velocity [*i.e.*, changes in the position of ocean isotherms (Burrows et al., 2011; Pinsky, Worm, Fogarty, Sarmiento, & Levin, 2013)]. Using this approach, we assess whether: 1.) Climate change leads to earlier phytoplankton blooms and earlier fish spawning; 2.) The sensitivity to climate change differs among trophic levels, causing a greater frequency of seasonal mismatches under climate change; 3.) Range shifts undertaken by fishes lessen the spatial extent and severity of seasonal mismatches with phytoplankton blooms; 4.) Changes in the frequency of mismatches between trophic levels are particularly pronounced at the extreme ends of their probability distribution, with these "extreme mismatches" potentially having outsized effects on fish recruitment success.

Materials and methods

Phytoplankton bloom phenology

Projections of phenology were produced using simulations from Geophysical Fluid Dynamics Laboratory Earth System Model 2 (GFDL ESM2M), a model with 50 depth layers and a nominal 1° latitudinal/longitudinal ocean resolution where the latitudinal resolution gradually decreases from 1° to 0.33° in areas equatorward of 28.5° N and S (Dunne et al., 2012, 2013). ESM2M includes an ocean biogeochemistry sub-model (Tracers of Ocean Phytoplankton with Allometric Zooplankton 2.0 [TOPAZ2.0]) with three phytoplankton functional groups that represent diazotrophs, small phytoplankton (pico- and nano-plankton), and large phytoplankton

(diatoms, dinoflagellates). We accessed publicly available data from ESM2M through the website of GFDL (https://www.gfdl.noaa.gov). The same datasets are also accessible through the website of the Coupled Model Intercomparison Project – Phase 5 (CMIP5; http://cmip-pcmdi.llnl.gov/cmip5), which archives models contributed to the fifth assessment report of the Intergovernmental Panel on Climate Change (IPCC). We analyzed ESM2M projections from a historical climate simulation (years 1861-2005) and the Representative Concentration Pathway (RCP) 8.5 emissions scenario (years 2006-2099). RCP8.5 is a high emissions scenario where anthropogenic influences on climate lead to an 8.5 W m^{-2} change in radiative forcing by 2100. Latitudes >40°N were primarily examined herein because this region contains the world's most productive fisheries and seasonal matches between trophic levels are more important at latitudes with pronounced seasonality (Cushing, 1990; Kristiansen, Drinkwater, Lough, & Sundby, 2011). We focused on the northern hemisphere due to model underestimation of summer mixed layer depth (MLD) in the Southern Ocean, which is a bias common to many models in CMIP5 (Sallée et al., 2013) and can affect phytoplankton phenology in the Southern Ocean (Henson et al., 2013; Supporting Information [SI] text; Figs. S2-S3).

Surface chlorophyll (0-10 m) from TOPAZ2.0 was outputted at a 5-day resolution. To facilitate comparisons with satellite observations, which were used to validate phytoplankton phenology patterns (SI text; Fig. S1), data were binned into 8-day time steps by averaging data when two TOPAZ2.0 observations fell within the 8-day period associated with observations from the SeaWiFS satellite. Chlorophyll concentration was then $\log_{10}$ transformed. Bloom initiation was defined as the date when surface chlorophyll from an ESM2M grid cell surpassed the 75th quantile of its annual range. We selected this quantile so approximately one season per year would be characterized by bloom conditions (Asch, 2013). Also, a relatively high threshold for defining bloom onset, such as the one used here, has been argued to be particularly useful when examining mismatches between trophic levels because mismatch dynamics correspond more closely with peaks in chlorophyll than with the initial increase in chlorophyll above the pre-bloom baseline (Brody, Lozier, & Dunne, 2013). To avoid classifying transient spikes in chlorophyll as blooms, a time series had to exceed this quantile for ≥2 time steps (*i.e.*, 8-day periods) within a 5-time step period. Bloom termination was identified as the date immediately before the time series dropped below the 75th quantile for at least 5 time steps. We also examined changes in bloom duration and magnitude because they can exacerbate seasonal

mismatches between trophic levels (Gotceitas, Puvanendran, Leader, & Brown, 1996; Kristiansen et al., 2011). Bloom duration was defined as the difference between bloom initiation and termination dates. Bloom magnitude was calculated as the geometric mean of chlorophyll during a bloom. In regions with multiple blooms per year, we focused on the first bloom detected.

Model performance was evaluated by comparing projections of phytoplankton bloom phenology produced with ESM2M to remotely sensed measurements of SeaWiFS surface chlorophyll concentration (SI text, Fig. S1). The performance of ESM2M when assessing bloom timing was similar to this model's performance when examining other characteristics of oceanic primary production (Dunne et al., 2013; Stock, Dunne, & John, 2014). Spatial correlations between SeaWiFS and ESM2M indicated that these two datasets were correlated at r=0.61 for bloom initiation, r=0.65 bloom termination, r=0.33 for bloom duration, and r=0.74 for bloom magnitude (Fig. S1).

In areas with predominantly fall or winter blooms, the discontinuity between December (days 335-365) and January (days 1-31) can affect calculation of phenological trends. To address this, we used a July-through-June year in such regions to compute mean dates of blooms and changes in phenology. We applied two criteria to pinpoint the grid cells from ESM2M where the July-June calendar year should be used (Asch, 2013): 1.) Interannual variance in bloom initiation and termination dates was larger when using a January-December calendar year than a July-June year. This increase in variance is an artefact of the January-December day of year discontinuity. 2.) The difference in variance between the January-December and July-June years was significant at p<0.05 based on the Levene test of equality of variances (Quinn & Keough, 2002). Fig. S4 shows regions where the July-June year was used to calculate trends in bloom initiation and termination.

We calculated mean changes in bloom initiation, duration, and magnitude by comparing the baseline years 1901-1950 with 2050-2099. All spatial means were calculated such that the area of each ESM2M grid cell was used as a weight to account for the fact that, in polar regions, a 1° latitude/longitude grid cell covers a smaller area than at lower latitudes. The baseline period was selected so that it contained years before any detectable changes in phytoplankton phenology (Fig. 1a). Also, a 50-year timespan was selected for the baseline and future periods to average across most modes of interannual and decadal climate variability ensuring that changes

were primarily due to anthropogenic climate forcing. Two-tailed t-tests were used to assess differences between these time periods. When mapping changes in phytoplankton and fish spawning phenology between these time periods, ESM2M data from the Black Sea were masked due to the fact that lower trophic level dynamics in this inland sea is not well resolved by the model (Stock et al., 2017).

We also examined relationships between bloom initiation, temperature, salinity, and stratification to explore oceanographic changes associated with shifts in phytoplankton phenology. Stratification was defined as the difference in potential density (ρ) between 5 and 100 m. During 1862-2099, we regressed bloom initiation dates against mean stratification during the median month of bloom initiation and the prior month. A 9-year running mean was used to smooth interannual variability and highlight long-term trends. A bandwidth of nine years was selected to remove the influence of decadal climate fluctuations while ensuring that an equal number of years were averaged before and after the target year of the running mean. We then partitioned the influence of stratification on bloom timing into effects of temperature and salinity following the approach of Capotondi et al. (2012). Changes in potential density at the sea surface ($\Delta\rho_0$) were calculated as:

$$\Delta\rho_0 = \rho_0(T_{II}, S_{II}) - \rho_0(T_I, S_I), \text{ where}$$

T and S are, respectively, the mean temperature and salinity at a nominal surface depth (*i.e.*, 0-10 m). Subscripts *I* and *II* refer to the baseline (1901-1950) and future (2050-2099) periods. The relative influence of temperature and salinity changes upon potential density changes were then estimated as:

$$\Delta\rho_{0,T} = \rho_0(T_{II}, S_I) - \rho_0(T_I, S_I)$$
$$\Delta\rho_{0,S} = \rho_0(T_I, S_{II}) - \rho_0(T_I, S_I)$$

These calculations were repeated for a depth of 100 m, so that changes in stratification could be calculated by subtracting $\Delta\rho_{100}$ from $\Delta\rho_0$. Similarly, changes in stratification due to the influence of temperature were calculated by subtracting $\Delta\rho_{100,T}$ from $\Delta\rho_{0,T}$, with this step also repeated to examine changes in stratification due to salinity.

Fish spawning phenology and trophic mismatches

Spawning phenology was modeled based on three eco-physiological principles: 1.) During baseline years (1901-1950), before discernible climate change impacts on bloom phenology (Fig. 1), we assumed fishes spawned on average synchronously with the start of the first bloom of the year; 2.) Interannual variations in fish spawning phenology reflected changes in cumulative degree days ($°D$) of sea surface temperature (SST) as has been shown in a variety ecosystems and for many fish species (Ware & Tanasichuk, 1989; Lange & Greve, 1997; Gillet & Quétin, 2006; Neuheimer & Mackenzie, 2014); 3.) In the absence of physiological adaptation, the threshold of $°D$ triggering spawning will remain unchanged under future conditions.

We computed $°D$ with the equation:

$$°D_t = °D_{t-1} + \max[T_t - T_0, 0], \text{ where}$$

$°D_t$ is the cumulative degree days at time t, T is daily SST, and T_0 is a baseline temperature below which fishes experience no gonadal development (Schwartz, 2013; Neuheimer & Mackenzie, 2014). T_0 was set at the climatological minimum SST from the baseline period since fish phenology is usually well adapted to temperatures in the fish's native range (Neuheimer & Mackenzie, 2014). During each baseline year, $°D$ were summed between bloom initiation and the date of the SST minimum detected within the 6 months preceding the bloom. Spatio-temporal spawning patterns have been found to be robust to the choice of date when $°D$ summation begins (Neuheimer & Mackenzie, 2014). The mean $°D$ at bloom initiation averaged over the baseline period was taken as the threshold for spawning. Assuming that this threshold was stable over time (*i.e.*, no physiological adaptation), dates of future spawning were calculated by summing $°D$ between the date of the SST minimum within 6 months preceding the bloom and the date when the spawning threshold was reached. For simplicity, we model spawning as occurring once per year, with all fish within a population spawning synchronously. Since warming temperatures clearly are not the predominant cue influencing the phenology of fall-spawning fishes (Pankhurst & Munday, 2011), $°D$ was not used to model fish phenology in areas where ESM2M projected predominantly fall blooms. Areas with fall blooms were defined as

those that had mean bloom initiation dates occurring between day of year 244-335 (September-November) during the baseline period. Some ESM2M grid cells with winter and spring blooms were interspersed among the regions where fall blooms predominated (Fig. S1a). Those grid cells were also excluded from this analysis to maintain spatial coherence across the region where fish reproductive phenology projections were made.

SST was used to calculate $°D$ because daily data were not outputted by ESM2M at other depths. Consequently, our modeling approach and results are most relevant to epipelagic fishes rather than demersal, mesopelagic, or bathypelagic species. However, changes in SST should be similar to the changes experienced by all fishes residing at depths above the permanent thermocline, since warming trends have been fairly uniform throughout this part of the water column (Rhein et al., 2013). To verify this pattern for the ESM2M model, we compared monthly changes in SST (0-10 m) between the baseline and future periods with changes in temperature at 100 m and 200 m (Fig. S5). The spatial pattern of warming across these three depths was significantly correlated ($0.73 \leq r \leq 0.95$) with each other and of a similar magnitude during all winter and spring months. Since these months generally corresponded to those used to calculate $°D$ in areas with spring and summer blooms, the consistent rate of warming across these depths indicates that our projections of phenological change among fishes should be similar regardless of the depth used for computing $°D$.

It has been shown that the spawning grounds of some fish species are defined by fixed geographic features and tend to be relatively stable over time (*e.g.*, salmon), whereas other species vary their spawning locations interannually in response to changing oceanic conditions (*e.g.*, bluefin tuna; Reglero et al., 2012). These behavioral modes are referred to as "geographic spawners" and "environmental spawners", respectively. In many ecosystems, ~40-50% of fishes behave similarly to geographic spawners in that they have not exhibited shifts in species distribution consistently with climate variations (Perry, Low, Ellis, & Reynolds, 2005; Hsieh, Reiss, Hewitt, & Sugihara, 2008; Hsieh, Kim, Watson, Di Lorenzo, & Sugihara, 2009; Nye, Link, Hare, & Overholtz, 2009). Among fishes whose distributions have varied over time, the magnitude and direction of historical changes in fish distribution have tracked climate velocity (Pinsky et al., 2013). Therefore, we used shifts in SST isotherms to project how spawning grounds of environmental spawners will change location. Based on mean annual SST, our study area was divided into isotherms bands with 2°C intervals, which represent the range of a fish's

preferred thermal habitat that its distribution will track (Pörtner & Peck, 2010; Habary, Johansen, Nay, Stefensen, & Rummer, 2016). The Atlantic and Pacific were assigned separate isotherm bands, assuming minimal exchange of species between basins. Within each isotherm band in each ocean basin, we calculated mean $°D$ and T_0. Future projections for environmental spawners used these mean parameters. Across 2.3% of our study area, the future period was characterized by non-analogous conditions where isotherm bands were warmer than any temperatures during the baseline period in our study area. No projections were made for environmental spawners in these regions because data on T_0 and mean $°D$ at the time of bloom initiation from outside of our study domain would be required to parameterize projections of phenological changes.

Mismatches where fishes spawned early (late) were calculated relative to bloom initiation (termination) date. We evaluated whether mean mismatches were significantly greater or less than zero using one-tailed t-tests.

The probability of extreme mismatches during baseline and future periods was calculated by dividing the number of mismatches $>|\pm30|$ days by the 50-year duration of each timeframe. We analyzed extreme mismatches associated with both early and late spawning relative to bloom timing. Extreme mismatches defined here as those exceeding 30 days are biologically significant because they are large relative to the duration of the egg and yolk-sac larvae stages of many fishes (Houde, 1987) and are, thus, more likely to result in food scarcity, reduced growth, heightened mortality, and potential recruitment failure. While egg and yolk-sac larvae duration varies greatly across marine and diadromous fish species (5-100 days for egg duration; Shanks and Eckert, 2005), most larvae will reach the "point of no return" where starvation induces inevitable mortality within 1-21 days (Helfman, Collette, Facey, & Bowen, 2009). At high latitudes, such as those included in our study region, durations of fish early life history stages tend to be longer than those observed at lower latitudes (Bradbury, Laurel, Snelgrove, Bentzen, & Campana, 2008). The 30-day threshold for defining extreme mismatches is meant to account for extended stage durations at polar latitudes. This threshold also corresponds to the point when deviations from mean phenological patterns have been shown to have strong population-level impacts on fished species across several ecosystems (Lindley et al., 2009; Mills et al., 2013; Auth, Daly, Brodeur, & Fisher, 2017). The ratio of probabilities of extreme mismatches between the future and baseline periods was used as an index of changes, such that ratios >1 indicated an increase in extreme mismatches and ratios <1 indicated a decrease in extremes.

Results

Between the years 1901-1950 and 2050-2099, bloom initiation is projected to shift earlier across 88.2% of the region north of 40°N (Fig. 2a,b). These shifts begin during the late 20th century in the Arctic, with changes then spreading southward and accelerating (Fig. 1a). By the end of the 21st century, bloom initiation occurs 23 days earlier on average in the northern Arctic [standard error (S.E.): ±0.05 days], with smaller mean phenological advances (-14.1±0.1 days S.E.) at 40-60°N.

The largest changes in spring/summer bloom duration occurred in the Arctic where blooms became on average 24.9 days (±0.1 days S.E.) shorter by the late 21st century (Fig. 2c,d; area-weighted, two-way t-test: t=276.0, p<0.0001, d.f.=391,448). Bloom magnitude is projected to decrease in the Arctic and much of the North Atlantic, with small, but statistically significant, increases in parts of the North Atlantic Drift, subpolar Pacific, and some marginal seas (Fig. 2e,f).

When examining individual ESM2M grid cells, bloom initiation was significantly correlated with upper-water column stratification across 95.6% of our study area, with stratification explaining ≥50% of variance in phenology in most regions (Fig. 3a,b). Correlations between stratification and phytoplankton phenology were negative nearly everywhere, indicating increased stratification was associated with earlier blooms. Stratification changes that affected bloom timing across most of the Arctic and North Atlantic were predominantly caused by freshening of surface waters (Fig. 3e,f). Temperature exerted a relatively strong effect on stratification and bloom timing in only two regions: 1.) Warming was the predominant influence on stratification changes in northwestern Pacific (Fig. 3d). 2.) South of Greenland enhanced atmospheric cooling of surface water associated with the slowing of the Atlantic Meridional Overturning Circulation influenced stratification, partially counteracting effects on stratification of freshening due to ice melt and enhanced precipitation (Manabe & Stouffer, 1993).

Between 1901-1950 and 2050-2099, our model indicates geographic spawners experience a mean (± S.E.) phenological advance of -33.0±0.3 days (median±S.E.: -42.2±0.4 days) due to accelerated gonadal development associated with increasing temperature (Fig. 4b). These changes among geographic spawners are projected to occur twice as fast as changes in bloom

initiation (Fig. 4a), resulting in spawning initiation occurring before the bloom across 86% of our study area (Fig. 5a,b). In contrast, spawning coincident with the bloom was observed across only 10% of the region during the 2050-2099 period for geographic spawners.

Regions with greater upper water column warming (Fig. S5) display larger mismatches among geographic spawners. One exception is the Arctic, where winter/spring warming is small, reflecting sea ice dynamics, but sizable mismatches between phytoplankton and geographic spawners still occur. Here modeled fish phenology changes rapidly because the $°D$ threshold for spawning is so low that even slight warming affects fishes.

Range shifts among environmental spawners were modeled such that spawning locations tracked 2°C-wide SST intervals that represent the range of a fish's preferred thermal habitat (Table 1; Fig. 6). Between 1901-1950 and 2050-2099, the spawning habitats of environmental spawners shifted northward by 58-1,397 km, with the largest shifts in the Pacific and at high latitudes (*i.e.*, isotherm intervals of 0-4°C). Since range shifts undertaken by environmental spawners maintain spawning grounds at a near constant temperature, environmental spawners exhibit smaller changes in phenology (mean change±S.E.: -10.8±0.4 days; Fig. 4c). The environmental spawners' mean (±S.E.) date of reproduction is separated from bloom initiation by 10.4±0.4 days during 2050-2099, indicating that reproduction occurs after bloom initiation, but before the bloom's end. Consequently, phenological mismatches are less widespread among environmental spawners (Fig. 5c,d). However, there are regions of stronger mismatches between environmental spawners and bloom timing reflecting the fact that temperature is not consistently the dominant factor controlling bloom timing (Fig. 3). Environmental spawners also reproduce asynchronously with the bloom in areas where changes in winter/spring SST (Fig. S5), which controls spawning phenology, lag or lead changes in mean annual SST (Fig. 6), which controls range shifts in our model. Overall, our analysis indicates that range shifts have the potential to reduce, but not completely eliminate, the heightened seasonal mismatches between trophic levels that are projected under climate change.

In addition to examining mean mismatches between phytoplankton and fish phenology, we investigated changes in extreme events defined as mismatches exceeding 30 days. Among geographic spawners, extreme mismatches were projected to occur ≥10 times more frequently during the 2050-2099 period across large swaths of the Arctic and North Pacific, with doubling of the frequency of extreme mismatches across most of the Atlantic (Figs. 7a and 8a,b). While

the frequency of extreme mismatches does not increase among environmental spawners when data are integrated over our entire study area (Fig. 7b), ≥5-fold increases in extreme mismatches were observed across several high latitude regions, including the Bering Sea, Sea of Okhotsk, much of the Pacific Arctic, and parts of the North Atlantic Drift (Fig. 8c,d).

Discussion

As the first study to produce projections of future mismatches between the seasonality of fishes and phytoplankton, we identified modest changes in phytoplankton phenology (*i.e.*, a mean phenological advance of -16 days) across latitudes >40° N. Among fishes with geographically fixed spawning grounds, changes in phenology occurred at a rate twice as fast as phytoplankton. Seasonal mismatches between these trophic levels will be further exacerbated by projected declines in spring bloom magnitude and duration. Phenological changes were more spatially heterogeneous, but generally slower, among fishes that were able to shift their spawning ground location in accordance with rising mean annual SST. Our finding that larger mismatches occur among geographic spawners than among environmental spawners suggests that species with fixed spawning grounds may be more vulnerable to climate change than species that can adapt by shifting their spawning location to track environmental conditions. However, compensation in environmental spawners fails when temperature is not the dominant driver of stratification changes, and both geographic and environmental spawners in many regions could be adversely affected by large increases in the frequency of "extreme" mismatches that exceed durations of 30 days. Compared to smaller mismatches between trophic levels, these extreme events are more likely to result in starvation of larvae, slower growth, and, ultimately, lower recruitment and fisheries productivity since the extent of the mismatch is related to its impact on a fish population (Durant et al., 2005; Schweigert et al., 2013). These impacts can stem from both mismatches where fishes spawn too early or too late relative to the seasonal cycle of plankton production (Schweigert et al., 2013).

A key question in interpreting our results is whether chlorophyll concentration is an appropriate metric for examining spring bloom timing in relationship to the match-mismatch hypothesis. Other alternative indicators of bloom timing could be derived from either depth-integrated primary productivity or phytoplankton carbon biomass (C_{phyt}). Friedland et al. (2012)

showed that net primary production was not strongly correlated with fisheries yields in large marine ecosystems (LMEs), whereas chlorophyll *a* concentration and fisheries yield exhibited a strong position correlation, varying between $0.59 \leq r \leq 0.70$ depending on how data were analyzed. The lack of strong correlation between primary production and fisheries yield reflects the fact that much primary productivity is consumed by heterotrophic bacteria and viruses and is not directly funneled into a fish-based food web (Pomeroy, Williams, Azam, & Hobbie, 2007). Also variations in the trophic transfer efficiency, food chain length, the proportion of benthic and pelagic fishes, and differences in fish metabolic demand in cold and warm ecosystems all add noise to the relationships between primary production and fisheries yield (Stock et al., 2017). Ultimately, the higher correlation between fisheries yield and chlorophyll indicates that this is a better indicator of bloom timing than primary production when examining match-mismatch dynamics. As for C_{phyt}, this variable was not saved on a sub-monthly basis during ESM2M simulations, so we could not directly examine changes in its phenology. At the interannual time scale, C_{phyt} has been shown to exhibit less variability than chlorophyll concentration because chlorophyll is influenced by both variations in phytoplankton production and the carbon-to-chlorophyll ratio (Behrenfeld et al., 2015). However, at the seasonal time scale, chlorophyll and carbon biomass are highly correlated across the North Atlantic ($0.76 \leq r \leq 0.93$; Behrenfeld, 2010). Breakdowns in these seasonal correlations occur primarily in summer at lower latitudes where light-driven photoacclimation has a greater impact on chlorophyll production. Since our study focuses primarily on higher latitudes, chlorophyll concentration should be a reliable indicator of bloom timing across most of our study region.

Our projections of changes in phytoplankton bloom phenology are consistent with a previous multi-model study of bloom characteristics (Henson et al., 2013; Henson et al., 2017) and with theoretical and empirical responses of blooms to enhanced stratification (Behrenfeld et al., 2006; Chiswell, Calil, & Boyd, 2015). The slower rate of phenological change among phytoplankton blooms compared to geographic spawners reflects the fact that warming temperatures have a smaller, indirect influence on phytoplankton bloom initiation, but a direct, physiological impact on fishes under our modeling framework. Beyond the classic critical depth hypothesis (Sverdrup, 1953), several hypotheses have been proposed in recent years examining the mechanisms underlying variations in bloom initiation phenology. These mechanisms include decoupling between phytoplankton and microzooplankton grazers as mixed layer depth deepens

in winter (Behrenfeld, 2010), reductions in light limitation on photosynthesis as water column mixing slows coincident (Townsend, Cammen, Holligan, Campbell, & Pettigrew, 1994; Huisman, van Oostveen, & Weissing, 1999; Huisman, Arrayás, Ebert, & Sommeijer, 2002; Taylor & Ferrari, 2011), and eddy-driven changes in the vertical and horizontal gradients of nutrient concentrations, stratification, and mixing, which can all influence bloom onset (Garçon, Oschlies, Doney, McGillicuddy, & Waniek, 2001; McGillicuddy et al., 2007; Mahadevan et al., 2012). While these hypotheses each emphasize distinct oceanic processes, they share commonalities in that they all assert that bloom phenology at mid-to-high latitudes is modulated by stratification and various types of mixing (*e.g.*, wind-driven mixing, eddy-driven mixing, heat flux-driven mixing, deep convection) (Ferreira, Hatún, Counillon, Payne, & Visser, 2015). This is consistent with the widespread pattern of synchronous variation between the extent of stratification and bloom initiation timing that we detected within ESM2M. With the exception of parts of the northwest Pacific, changes in salinity were the predominant driver of heightened stratification and its resultant effect on bloom timing, while temperature played a more limited role. This finding is similar to the results of Song et al. (2010) and Song, Ji, Stock, Kearney, & Wang (2011) who also found that spring blooms began earlier in the northwest Atlantic during years characterized by earlier stratification onset due to fresher surface salinity. In this region, Song et al. (2010, 2011) found that SST had a small influence on fall bloom timing and no notable effect on spring blooms.

This contrasts with the predominant role of temperature affecting fish phenology in our modeling framework, leading to the widespread trophic mismatches among geographic spawners. This aspect of our model is bolstered by a recent meta-analysis indicating that, across >1,000 animal taxa whose phenology has been studied, temperature exerted a larger influence on phenological processes than other climatic variables (Cohen, Lajeunesse, & Rohr, 2018). Tracking changes in the distribution of isotherms allowed environmental spawners in our model to reproduce in sync with the bloom across many regions, but synchrony was not observed everywhere due in part to the salinity-induced changes in stratification (Figs. 3, S6) and bloom timing (Fig. 2).

Seasonal mismatches between trophic levels are likely to be exacerbated by the declines in bloom magnitude and spring/summer bloom duration indicated by our model, since larval fishes are more resilient to mismatches when overall levels of primary and secondary production

are high (Gotceitas et al., 1996). Despite our projection of shorter spring/summer blooms in the Arctic, the overall growing season in this region may increase since the area of the Arctic with both spring and fall blooms, interspersed by stratified summer conditions, could expand under climate change (Ardyna et al., 2014).

Our results are consistent with empirically observed changes in fish spawning phenology from regions where sufficiently long time series exist to evaluate trends. In the North Sea, the seasonal peak in the abundance of fish and invertebrate larvae has changed more rapidly during recent decades than changes among other types of plankton (Edwards & Richardson, 2004). In the English Channel, the period of occurrence of larval fishes advanced by 12 weeks over the last 25 years, whereas the onset of the bloom of most zooplankton taxa, with the exception of *Acartia* spp., remained steady or changed at a slower rate (Reygondeau, Molinero, Coombs, MacKenzie, & Bonnet, 2015). In the California Current, the majority of larval fish species exhibited larger decadal trends in seasonal occurrence than did zooplankton (Asch, 2015). Seventy-six of 81 ichthyoplankton taxa in the German Bight advanced their seasonal occurrence during warm years, while the timing of the spring bloom in this region was relatively insensitive to SST (Greve, Prinage, Zidowitz, Nast, & Reiners, 2005; Wiltshire et al., 2008), suggesting that climate change is likely to induce mismatches between trophic levels. Collectively, these examples illustrated that, even though there is no global database of fish phenology available to validate our results, most ecosystems with multidecadal time series of both fish and plankton phenology show trends indicative of an increased frequency of seasonal mismatches (Edwards & Richardson, 2004; Asch, 2015; Reygondeau et al., 2015). These observations of past changes are consistent with the future projections of our model.

While fish reproductive phenology and recruitment success have been linked with phytoplankton bloom phenology in multiple regions (Platt et al., 2003; Schweigert et al., 2013; Malick, Cox, Mueter, & Peterman, 2015), a greater understanding of how zooplankton population dynamics and phenology influence these processes would improve the mechanistic understanding of mismatch phenomena. However, our ability to understand and model zooplankton phenology across basin-wide scales is limited by the relative dearth of phenological time series available for zooplankton and the fact that the time series that exist are not spatially representative, thus, constraining our ability to assess model skill (Ji, Edwards, Mackas, Runge, & Thomas, 2010; Mackas et al., 2012). Nevertheless, some literature on this subject provides us

with insight into how climate change may influence the phenology of micro- and mesozooplankton and how this may in turn impact both phytoplankton blooms and fish reproduction.

In the case of microzooplankton, mesocosm experiments have demonstrated that microzooplankton metabolism is upregulated by warming temperatures to a greater extent than phytoplankton, resulting in increased synchrony between phytoplankton blooms and peaks in microzooplankton abundance (O'Connor, Piehler, Leech, Anton, & Bruno, 2009; Aberle, Bauer, Lewandowska, Gaedke, & Sommer, 2012). Similarly, according to the dilution-recoupling hypothesis (Behrenfeld, 2010), increased stratification and the shoaling of the mixed layer under climate change would be expected to lead to higher encounter rates between phytoplankton and microzooplankton, which would in turn allow microzooplankton to better control phytoplankton populations. Increased top-down control by microzooplankton may negatively impact mesozooplankton if there is competition between these two size classes of grazers, but it could also have a minimal effect on mesozooplankton in cases where they also graze on microzooplankton (Aberle et al., 2012).

Interactions between mesozooplankton and lower trophic levels under climate change will ultimately depend on whether mesozooplankton are liable to change their own phenology in sync with their prey. Based on current evidence, this seems questionable since mesozooplankton phenology has been shown to be poorly correlated with phytoplankton bloom phenology in the North Sea, English Channel, Northeast Pacific, Northwest Pacific, and off the east coast of Canada (Mackas et al., 2012). Similarly, the mesocosm experiments of Aberle et al. (2012) indicated that micro- and mesozooplankton phenology exhibited different responses to warming temperatures. This information combined with the fact that both mesozooplankton and fish reproductive phenology are highly sensitive to temperature (Pankhurst & Munday, 2011; Mackas et al., 2012; Dam & Baumann, 2017) and tend to exhibit high phenological variability (*i.e.*, >1 month; Greve et al., 2005; Genner et al., 2010; Ji et al., 2010; Mackas et al., 2012; Asch, 2015) suggests that seasonal mismatches may be more likely to occur between phytoplankton and zooplankton phenology rather than between zooplankton and their larval fish predators. This hypothesis is supported by the work of Friedland, McManus, Morse, & Link (2018), which shows that there is greater similarity in the responses of fishes and copepods to climatic forcing than there is between either of these groups and phytoplankton. Similarly, fishes and crustaceans

in marine and freshwater environments in the United Kingdom are both projected to undergo much larger changes in phenology than phytoplankton (Thackeray et al., 2016).

Regardless of which trophic levels are the ones subjected to mismatches, the outcome may be the same and consistent with the results discussed herein. If seasonal mismatches between phytoplankton, microzooplankton, and mesozooplankton lead to decreased mesozooplankton production, then larval fishes will experience a decline in prey availability even if their seasonal production patterns are in sync with those of mesozooplankton.

The magnitude of trophic mismatches estimated by our study will be modulated by several factors, including the extent of future warming, whether fish range shifts lag or lead climate velocity, duration of the spawning period, and the sensitivity of fish phenology to additional biological and environmental factors (*e.g.*, photoperiod; hydrography; prey availability; size, age, and genetic structure of fish stocks; variations in migration routes; social interactions among fish; endogenous factors). Also, the impact of phenological mismatches on fish population dynamics will depend on whether a fish species has a generalist or specialist diet (Durant et al., 2007) and whether the plankton species represented in a bloom provide high quality food for fish larvae (Beaugrand et al., 2003; Peterson, 2009). Regarding this latter point, diatom blooms play a particularly important role in transferring energy between primary producers and fishes. Temperature does not have a predominant effect on diatom phenology (Edwards & Richardson, 2004; Mackas et al., 2012; Guinder et al., 2017; Bermejo, Helbling, Durán-Romero, Cabrerizo, & Villafañe, 2018), leading to a greater potential for mismatches with higher trophic levels. Some adverse consequences of increased mismatches may be countered by adaptation of fishes to changing temperatures (Donelson, Munday, McCormick & Pitcher, 2012) or decreased density dependence of mortality at the juvenile stage reflecting less interspecific competition for resources (Houde, 2008; Reed, Grøtan, Jenouvrier, Sæther, & Visser, 2013). In absence of both of these compensatory mechanisms, trophic mismatches and their impact on recruitment could potentially lead to declines in fish populations of a comparable or greater magnitude to the direct effects of warming temperatures (Pörtner & Farrell, 2008; Cheung, Reygondeau, & Frölicher, 2016; Comte & Olden, 2017), ocean acidification (Munday et al., 2009, 2010; Dixson, Munday, & Jones, 2010), and changes in primary and secondary production on fishes (Stock et al., 2017).

Population-level impacts of phenological change can occur through a variety of mechanisms. Shifts in spring spawning phenology to earlier in the year cause there to be fewer hours of daylight available when visual predators are able to hunt, leading to depressed growth rates among larval fishes (Shoji et al., 2011). This effect of decreased hunting time could be amplified by trophic mismatches, which could lead to a lower concentration of prey during time periods of high metabolic demand among larvae. Since mortality rates in fishes are size dependent (Anderson, 1988), slower growth can have a compounding effect on larval survival and year class strength. Such impacts of phenological mismatches on recruitment have been demonstrated across a variety of species, including Pacific herring (Schweigert et al., 2013), coho salmon (Logerwell, Mantua, Lawson, Francis, & Agostini, 2003; Chittenden et al., 2010), Atlantic cod (Cushing, 1990; Wieland, Jarre-Teichmann, & Horbowa, 2000; Beaugrand, Brander, Lindley, Souissi, & Reid, 2003), haddock (Platt et al., 2003), mussels (Barth et al., 2007), and barnacles (Barth et al., 2007). There are also many documented cases where changes in seasonal synchrony between trophic levels and precipitating recruitment failure have led to declines in populations of marine organisms, sometimes to the point of near ecological extinction (Beare & McKenzie, 1999; Winder & Schindler, 2004; Costello, Sullivan, & Gifford 2006; Sullivan, Costello, & van Keuren, 2007). Not only can this affect fishery catch, but persistent mismatches can alter the carrying capacity of fish stocks delaying mandated stock rebuilding times of overfished species (Holt & Punt, 2009). Broader ecosystem impacts of phenological shifts and trophic mismatches include changes in connectivity between meta-populations (Carson, López-Duarte, Rasmussen, Wang, & Levin 2010), reformulation of food web dynamics (Philippart et al., 2003), decreased energy flow to top predators (Sydeman et al., 2006; Frederikson, Elston, Edwards, Mann, & Wanless, 2011; Burthe et al., 2012; Keogan et al., 2018), reduced provision of ecosystem services (Burkle, Marlin, & Knight, 2013), and changes in biodiversity (Willis, Ruhfel, Primack, Miller-Rushing, & Davis, 2008; Usinowicz et al., 2017).

Fishes with a limited capacity to adjust their spawning location under climate change were projected to experience the largest mismatches between trophic levels. An inability to track climate velocity can result from philopatry (*i.e.*, site fidelity), a life history with limited dispersal capacity, physical barriers to dispersal, or a lack of appropriate habitat in regions where fishes have dispersed. Resource managers may be able to ameliorate impacts of mismatches by facilitating population connectivity and dispersal between patchily distributed habitats.

Conservation and restoration of fish habitat, such as seagrass beds and salt marshes, could facilitate migration of geographic spawners to new spawning and nursery grounds, allowing them to keep pace with climate velocity. This would alleviate trophic mismatches among geographic spawners in the regions where there is good alignment between future bloom timing and reproduction by environmental spawners, but it would not prevent mismatches in other regions (*e.g.*, Bering Sea, Sea of Okhotsk, East Siberian Sea, Laptev Sea, and the North Atlantic Drift; Fig. 3c,d). Conservation of essential fish habitat would also have many complementary benefits that can help ecosystems and coastal communities adapt to climate change impacts. For example, coastal wetlands, which play a key role in supporting juvenile fishes, contribute to coastal resilience in the face of climate change by protecting coastlines from sea level rise, attenuating wave energy from more intense storms projected to occur under climate change, and taking up CO_2 via photosynthesis and thus providing a localized buffer zone reducing ocean acidification impacts (Roberts et al., 2017).

Even with the implementation of management measures designed to facilitate migration of geographic spawners, increases in extreme mismatches remain a concern given their potential to have a disproportionately large impact on fish recruitment. While environmental spawners did not display an increase in extreme mismatches when data were averaged across our study region, the frequency of extreme mismatches was projected to increase by >500% in some ocean basins even when fishes shifted their range in concert with climate velocity (Fig. 8c,d). This result is consistent with other studies that have also documented regional-to-global increases in extreme events, including heat waves, precipitation extrema, droughts, and the intensity of tropical storms (Hartmann et al., 2013; Oliver et al., 2018). In addition to extreme mismatches between trophic levels, other types of extreme events, such as storms and ocean heat waves, can produce stress responses in fishes where reproduction is inhibited (Pankhurst & Munday, 2011). Mismatches between trophic levels and phenological shifts of the same magnitude as those classified here as "extreme" have caused large alterations in the species composition and distribution of zooplankton and ichthyoplankton (Brodeur et al., 2006; Mackas, Peterson, Ohman, & Lavaniegos, 2006), reduced and delayed benthic invertebrate recruitment (Barth et al., 2007), caused reproductive failure among seabirds (Sydeman et al., 2006), decreased fishery profitability (Mills et al., 2013), and resulted in fishery collapse (Lindley et al., 2009). In some cases, selective pressure associated with survival of extreme events can lead to rapid

evolutionary responses, which may help populations withstand the effects of climate change (Campbell-Staton et al., 2017). Overall, the prevalent increase in extreme trophic mismatches projected here is an indicator that future work on phenological shifts should focus on changes in the tail ends of statistical distributions in addition to mean changes.

In conclusion, phenological mismatches between trophic levels are projected to increase under climate change because different oceanic factors cue phytoplankton blooms and fish reproduction. Range shifts in fish spawning grounds act to ameliorate the extent of these mismatches across many mid-to-high latitude regions, indicating that species whose dispersal capacity is constrained may be among the most vulnerable to this particular climate change impact. As a result, greater conservation of species that behave similarly to geographic spawners is needed to ensure their future persistence. Increases in mismatch events exceeding 30 days were especially pronounced among geographic spawners, but were also regionally important for environmental spawners. More frequent extreme mismatches can lead to greater recruitment variability among commercially important fishes, which may need to be accounted for in stock assessments. The applicability of our results to particular fish species will depend on how closely a given species' behaves like an environmental or geographic spawner and whether the fish's spawning phenology is influenced by additional environmental or endogenous factors that were beyond the scope of this study. However, we anticipate that our modeling approach will be broadly applicable to a range of fish species since temperature is among the most common environmental variables to affect spawning timing. This study also provides a baseline to be built upon by future work incorporating additional environmental and biotic factors. Furthermore, the approach used here could be broadly applied to other terrestrial, aquatic, and marine taxa since temperature measured in $°D$ is a common control on animal and plant phenology (Wolkovich et al., 2012; Schwartz, 2013).

Acknowledgments

by examining the sources of the model bias in Southern Ocean phytoplankton phenology. D. Tommasi, C. Petrik, M. Payne, and one additional anonymous reviewer provided useful suggestions that improved the manuscript.

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Table 1: Shifts in the area-weighted mean latitude of sea surface temperature isotherms between 1901-1950 and 2050-2099. Mean ± standard errors of isotherm shifts are shown. Latitudinal shifts in isotherms are a proxy for range shifts in the spawning grounds of fishes. Positive numbers are indicative of northward shifts.

	Latitudinal shift (km)	
Isotherm band (°C)	Atlantic	Pacific
<0	348.0 ± 11.5	218.7 ± 12.2
0-2	907.4 ± 33.9	1396.9 ± 39.7
2-4	223.6 ± 33.4	911.2 ± 49.1
4-6	323.8 ± 29.9	471.3 ± 18.9
6-8	76.0 ± 22.5	238.0 ± 15.9
8-10	105.8 ± 19.4	307.5 ± 15.5
10-12	115.0 ± 21.3	446.9 ± 21.0
12-14	139.5 ± 16.4	247.5 ± 17.9
14-16	160.4 ± 8.8	
16-18	142.3 ± 9.1	
>18	57.6 ± 3.3	

Figure captions

Figure 1. Spatially averaged time series of phytoplankton bloom characteristics for the RCP8.5 scenario. Characteristics shown include (a) bloom initiation date, (b) duration, and (c) magnitude. Units for changes in bloom initiation and duration are days. Gray areas indicate the 95% confidence intervals of the time series mean.

Figure 2. Spatial changes in phytoplankton bloom characteristics under the RCP8.5 climate scenario. Maps of changes are shown for (a, b) bloom initiation phenology, (c, d) bloom duration, and (e, f) bloom magnitude. These maps compare the baseline (1901-1950) and future (2050-2099) periods. In (a, b), negative numbers indicate blooms that occur earlier in the year, while positive numbers indicate delayed phenology. Units for changes in bloom initiation and duration are in days. Changes in bloom characteristics significant at $p<0.05$ are indicated by black contour lines (*i.e.*, white or pale colored areas outside the contour lines are not statistically significant). In regions with multiple blooms per year, data are shown for the first bloom identified during each calendar year (typically a spring or summer bloom). Inland seas and some coastal areas where no data from ESM2M are available are shown in black here and in subsequent figures.

Figure 3. Influence of upper-water column stratification on the timing of bloom initiation. (a, b) R^2 from regressions between bloom initiation dates from the years 1862-2099 and mean stratification during the median month of bloom initiation and the month beforehand. Stratification is defined as the difference in potential density between 5 and 100 m. Greater stratification was associated with earlier bloom initiation in all regions except those with cross-hatching. Dark gray areas indicate regions with depths shallower than 100 m. Also shown are the contributions of (c, d) temperature and (e, f) salinity to changes in stratification between the baseline (1901-1950) and future (2050-2099) periods. Color bar scale differs between (c, d) and (e, f), reflecting the stronger influence of salinity on changes in stratification.

Figure 4. Histograms of mean phenological changes (units: days) between the years 1901-1950 and 2050-2099. (a) Bloom initiation dates; (b) geographic spawners; (c) environmental spawners. Each datum in the histograms represents a 1° latitude/longitude grid cell from the Earth System Model (ESM2M). In (a), (b), and (c), negative (positive) numbers indicate phenological events that shift earlier (later) in the year. Thick, black lines are the median of each histogram; thin, dashed, black lines denote a change in phenology of 0 days.

Figure 5. Seasonal mismatches among spawning fish and phytoplankton blooms. Maps of mean mismatches between the timing of phytoplankton blooms and reproduction by (a, b) geographic spawners and (c, d) environmental spawners are shown for the years 2050-2099. Negative values indicate the number of days that fish spawn before the start of the bloom, whereas positive values indicate the number of days that fish spawn after the bloom ends. Zero denotes locations with synchronous spawning and blooms (*i.e.*, spawning occurs between bloom initiation and termination). Red and blue contours enclose regions where mismatches were significantly different from zero (*i.e.*, white or pale colored areas outside the contour lines are not statistically significant). Medium gray areas outside of continental landmasses show regions where no future projections of mismatches were made due to a predominance of fall blooms. Dark gray areas in (c, d) indicate regions where no projections of mismatches were made for environmental spawners due to a lack of analogous sea surface temperature (SST) conditions that occurred during the baseline period.

Figure 6. Maps of mean sea surface temperature (SST) isotherms during (a,b) 1901-1950 and (c, d) 2050-2099. Changes in annual isotherm locations are used to track shifts in the spawning grounds of fishes classified as environmental spawners. Temperatures >20°C are included in the 18-20°C isotherm band. Darker gray regions were not included in future projections of the phenology of environmental spawners due the predominance of fall phytoplankton blooms.

Figure 7. Percentage of the North Atlantic and North Pacific that experiences extreme mismatches each year. The black and red lines show projections for the North Atlantic and North Pacific, respectively. Extreme mismatches >30 days are calculated as the difference between bloom timing and spawning dates of (a) geographic and (b) environmental spawners. The 95% confidence intervals of these time series are shown in gray and pink shading for the Atlantic and Pacific, respectively. Note that y-axes differ between (a) and (b), with nearly a 2x greater percentage of extreme mismatches among geographic spawners by 2100.

Figure 8. Changes in extreme mismatch frequency between future (2050-2099) and baseline (1901-1950) periods. Extreme mismatches are calculated as the difference between bloom timing and spawning dates of (a, b) geographic and (c, d) environmental spawners. Changes in mismatches >30 days are shown as ratios between the frequency of these events occurring during the future and baseline periods. A ratio of 2 indicates a doubling of extreme mismatches, whereas a ratio of 0.5 indicates a 50% decrease in the probability of extreme mismatches. Light and dark gray regions are the same as in Fig. 5.
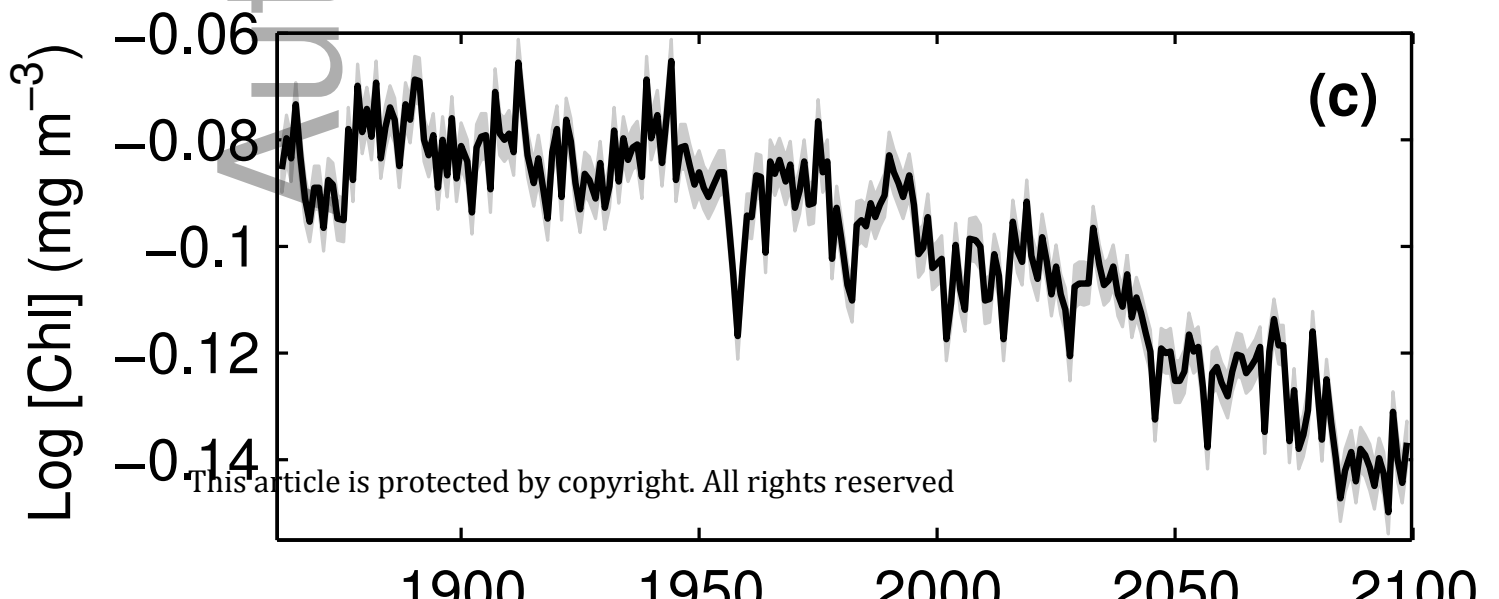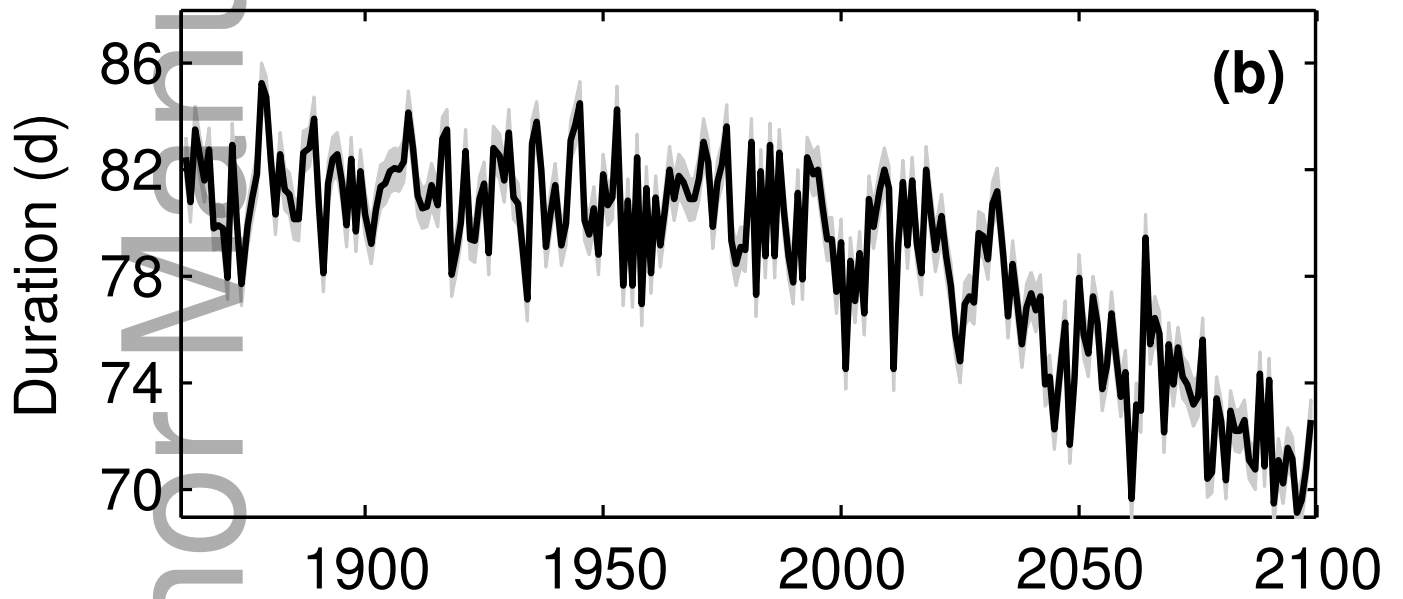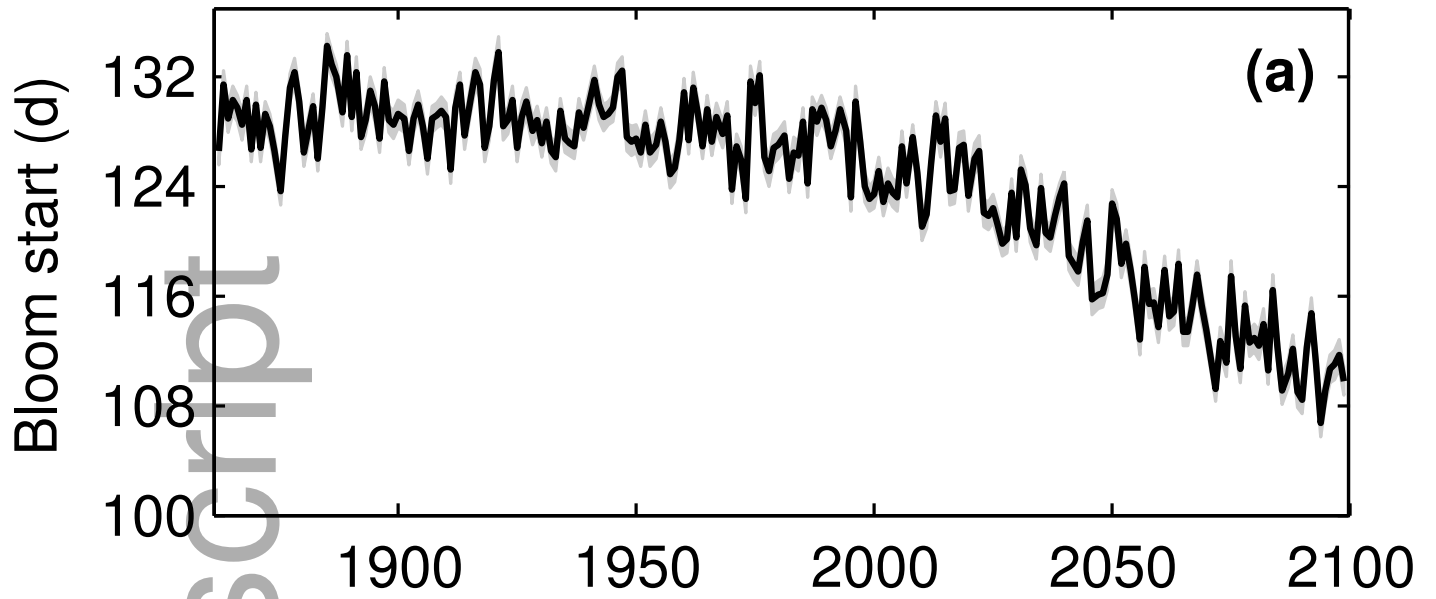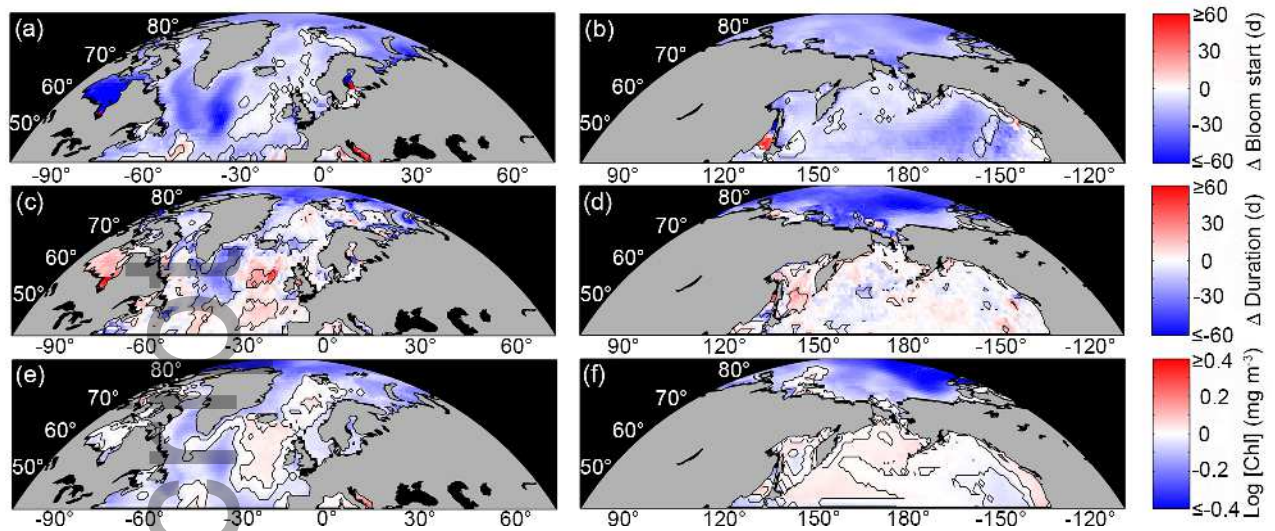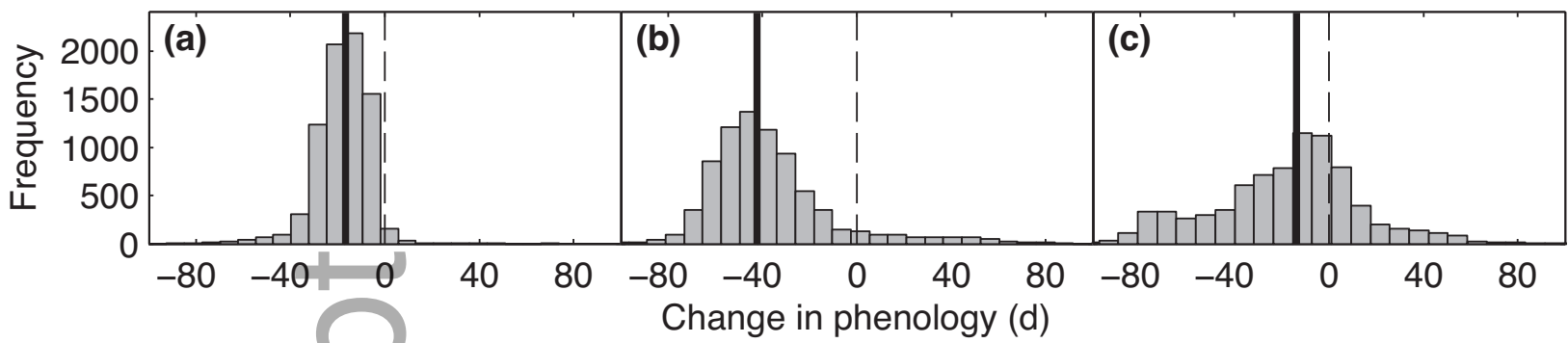
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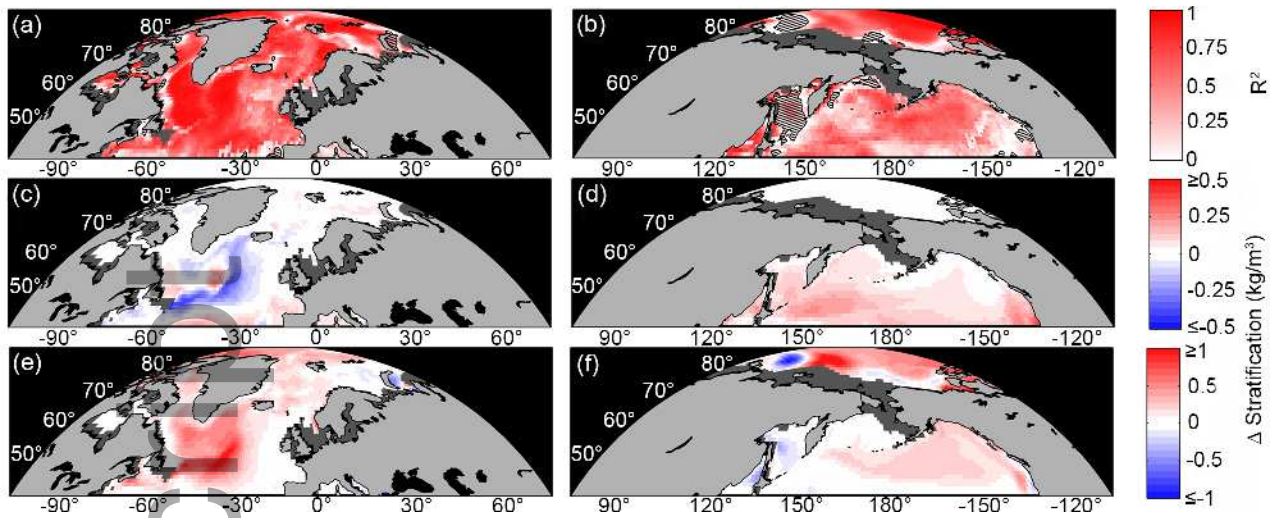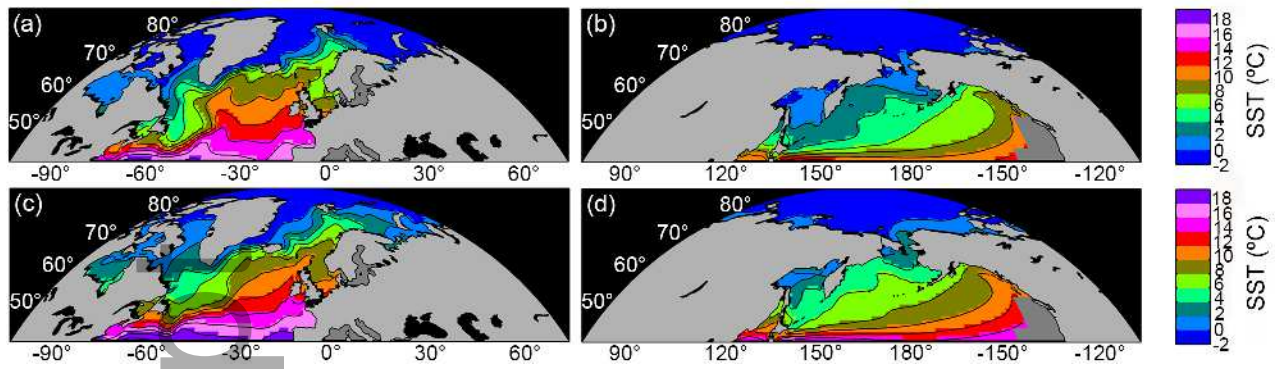
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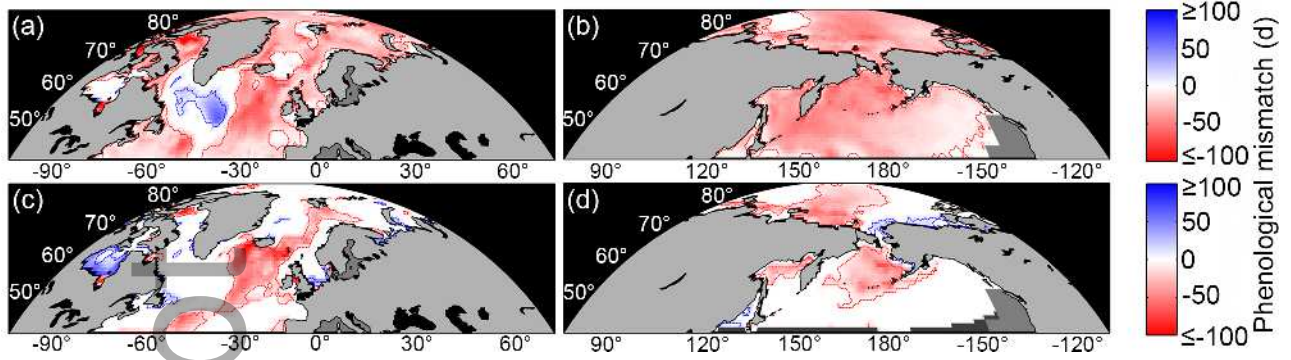
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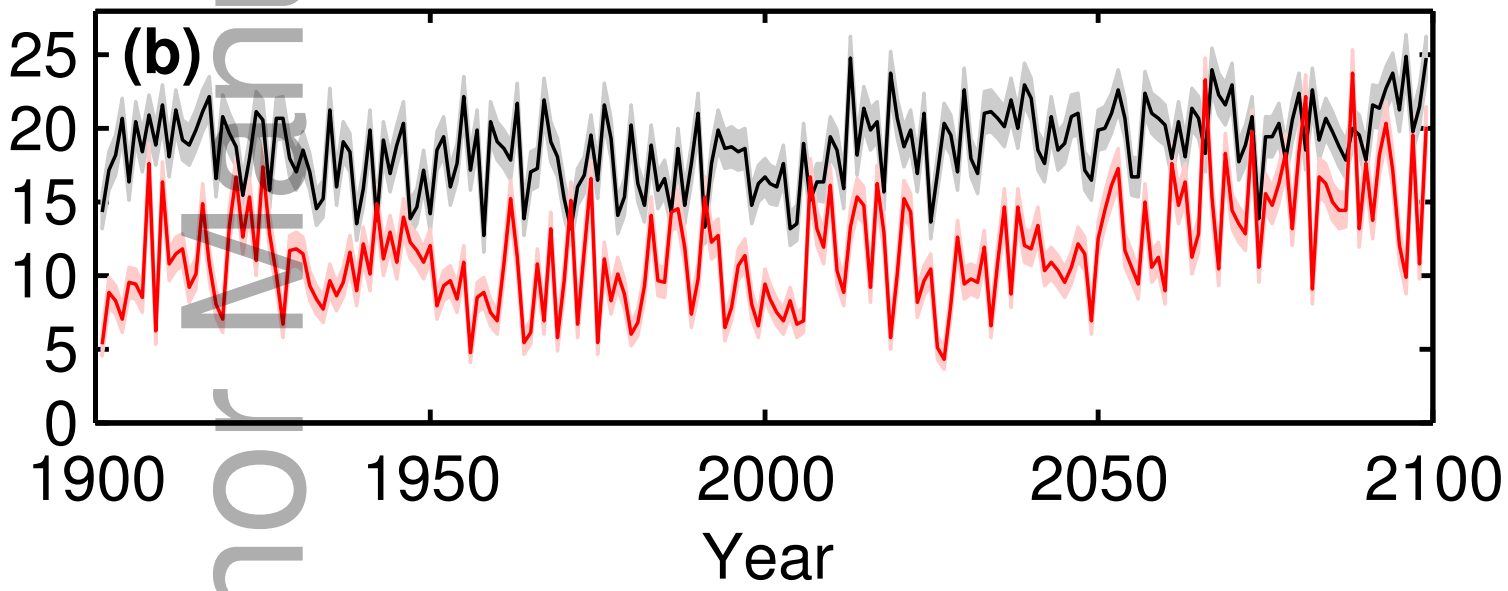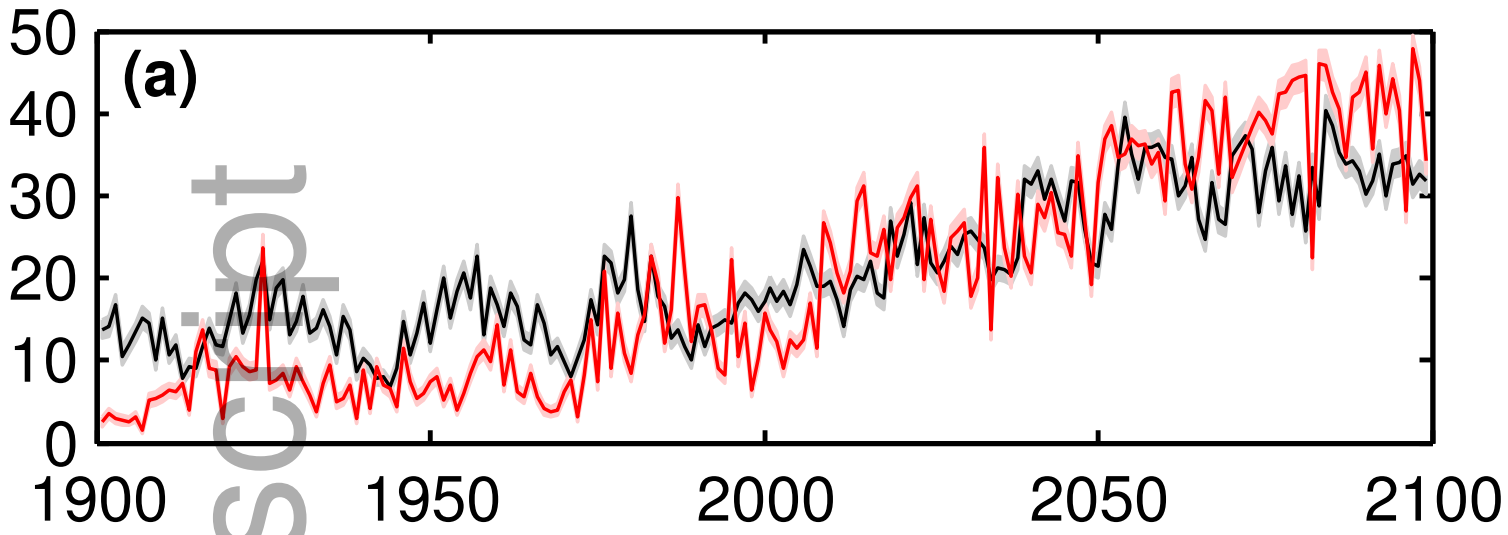
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