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The accuracy of climate models' simulated season lengths and the effectiveness of grid scale correction factors

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Abstract. Global climate change is expected to impact biological populations through a variety of mechanisms including increases in the length of their growing season. Climate models are useful tools for predicting how season length might change in the future. However, the accuracy of these models tends to be rather low at regional geographic scales. Here, I determined the ability of several atmosphere and ocean general circulating models (AOGCMs) to accurately simulate historical season lengths for a temperate ectotherm across the continental United States. I also evaluated the effectiveness of regional-scale correction factors to improve the accuracy of these models. I found that both the accuracy of simulated season lengths and the effectiveness of the correction factors to improve the model's accuracy varied geographically and across models. These results suggest that regional specific correction factors do not always adequately remove potential discrepancies between simulated and historically observed environmental parameters. As such, an explicit evaluation of the correction factors' effectiveness should be included in future studies of global climate change's impact on biological populations.

Key words: Allonemobius socius; *AOGCM; climate change; model accuracy; season length.*

Introduction

How global climate change will impact both wild and domesticated biological populations is of interest to evolutionary ecologists (Walther et al. 2002, Parmesan and Yohe 2003), agriculturalists (Fuhrer 2003, Nardone et al. 2010), conservationists (McCarty 2001, Thomas et al. 2004), economists (Nordhaus 2001, Stern 2006), policy makers (Jaffe et al. 2009, Ekholm et al. 2010), and the general public (Reiner et al. 2006, Hamilton and Keim 2009). Much of this work involves comparing the environmental tolerances of a species to its predicted future environmental conditions (i.e., projecting climate envelopes; Pearson and Dawson 2003, Thomas et al. 2004). In these studies, local extinctions are expected whenever future environmental conditions within the focal organism's current range fall outside its environmental tolerances. Similarly, range expansions are expected whenever future environmental conditions outside the focal organism's current range fall within its environmental tolerances (assuming unlimited dispersal capability). Together, these local extinctions and range expansions allow researchers to predict how species distributions might shift over time as a result of global climate change.

Although environmental tolerances are undoubtedly an important mechanism through which global climate change will impact biological populations, other mechanisms are likely to be important as well. One of these "other mechanisms" involves changes in the length of a population's growing season (Linderholm 2006, Christidis et al. 2007). The general warming trend predicted by most climate change scenarios (Nakicenovic and Swart 2000), should increase the amount of time many populations have to complete growth and reproduction. Such increases could lead to shifts in both evolutionary (Zani 2008, Kivela et al. 2009) and ecologically (White et al. 1999, Hudson and Henry 2009) relevant parameters. These shifts are most likely to occur in species with temperature dependent physiologies (i.e., where growth and reproduction rates are a function of external temperatures); and in populations located in temperate regions (i.e., where season lengths are relatively short).

For example, the striped ground crickets of the *Allonemobius socius* species group (Traylor et al. 2008) are small bodied terrestrial ectotherms found throughout the continental United States and southern Canada. Differences in the length of these crickets' natal growing seasons are closely associated with variation in several crucial life-history traits, including nymphal development time (Mousseau 1988), body size (Mousseau and Roff 1989*a*), wing dimorphism (Mousseau and Roff 1989*b*), and diapause incidence (i.e., the proportion of individuals that enter an arrested physiological state; Mousseau and Roff 1989*a*, Winterhalter and Mousseau 2007). Determining how these life-history characters will respond to increases in the length of the growing season is a critical step toward our understanding how global

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climate change will impact this particular group, as well as other temperate ectothermic species.

Climate models are an important tool for anticipating the potential environmental changes that will occur over the next century and beyond. One class of models that are frequently used in these projections is called the atmosphere and ocean general circulating models or AOGCMs. AOGCMs divide the planet into a series of grids, and then use previously established mathematical descriptions of both the internal dynamics (e.g., ocean currents and carbon cycles) and the external forcings (e.g., solar radiance, CO_2 emissions) that contribute to climate in order to simulate historical and future environmental conditions. These models are considered one of the most sophisticated physical climate models currently available, and are the primary models used in international climate policy assessments (IPCC 2007). One of the strengths of these models is that they are capable of simulating historical environmental conditions at the continental scale (Christensen et al. 2007). These results suggest that the models' mathematical dynamics adequately approximate climatic processes, and that they will be able to accurately simulate future conditions at the continental scale as well.

However, the ability of AOGCMs to simulate historical conditions at the scale of individual grids is considerably lower (Giorgi 2005). This deficiency is particularly significant to those interested in predicting the response of biological populations to global climate change for two reasons. First, the entire range of many species is substantially less than a continent (Brown et al. 1996). As such, applying broad-scale environmental predictions to narrowly distributed species may not be appropriate. And second, species that have relatively broad ranges often exhibit geographic variation for a number of phenotypes within their distributions (Endler 1977, Morrison and Hero 2003). How these regional level differences might be affected by global climate change cannot be adequately evaluated using continental-scale projections.

To compensate for these inaccuracies (i.e., model biases), regional-scale correction factors are often applied to a model's raw output (Giorgi and Francisco 2000, Kearney and Porter 2004, Lawler et al. 2009). These correction factors effectively compare the model's simulated historical conditions to the historically observed conditions (usually obtained from weather stations), and then apply the differences to the model's future predictions. In this manner, the magnitude of the change predicted by the model is maintained, while the discrepancies between the simulated and observed environmental conditions (i.e., the model's inaccuracies) are reduced or eliminated. Although these correction factors have been applied to a variety of environmental parameters (e.g., average temperature, precipitation, percent sunlight; Walther et al. 2002, Parmesan 2006), they have not been made within the context of predicting future season lengths of temperate ectotherms.

The purpose of this study was three-fold: (1) to determine the ability of AOGCMs to simulate the historical season lengths of a temperate ectotherm at the regional geographic scale; (2) to generate regional level correction factors for the environmental parameters that contribute to season length; and (3) to evaluate the ability of these correction factors to improve the accuracy of the models. I chose the striped ground crickets from the *A. socius* species group as my focal organism because of their wide distribution (Howard 1983, Traylor et al. 2008), and the intimate relationship between the length of their growing season and their life-history characters (Mousseau and Roff 1989*a*, Winterhalter and Mousseau 2007).

Methods

Season length calculations

Because of their temperature dependent physiology, the length of the growing season for temperate ectotherms is typically measured in accumulated thermal units or degree-days (Bonhomme 2000). Degree-days are dependent on both the external environmental conditions and the range of temperatures that permit the focal organism to metabolize and grow. For example, the upper and lower thermal thresholds for growth in the *A. socius* species group are 35°C and 13°C, respectively (Mousseau 1988). If these crickets were reared at a constant temperature of 23°C for 24 hours, then they would accumulate 10 degree-days greater than 13°C (i.e., 23°C–13°C = 10 deg-days > 13°C). Likewise, if they were reared at 33°C for 24 hours, they would accumulate 20 degree-days.

Unlike most laboratory conditions, temperatures in the wild fluctuate both daily and seasonally. To approximate the number of degree-days accumulated by the *A. socius* species group in a given year (i.e., the season length), I used Allen's dual sine wave methodology (Allen 1976). Briefly, this method fits a series of sine waves to the daily maximum and minimum temperatures experienced in a given habitat over an entire year. The number of degree-days accumulated during this period is set equal to the area underneath these sine wave curves that also fall within the organism's thermal limits for growth.

For this study, I assumed that the upper and lower thermal limits for growth of the *A. socius* species group were constant across their entire range (upper limit = 35°C, lower limit = 13°C). The daily maximum and minimum temperatures were obtained from either the output files of an AOGCM in the case of the simulated season lengths, or from weather stations in the case of historical observations.

Simulated data

The primary climate model examined in this study was the AOGCM produced by the Geophysical Fluid Dynamics Laboratory (GFDL) designated cm2.0 (Delworth et al. 2006). I chose this particular model because the arrangement of its grids happened to correspond to regional differences in the life-history strategies of the *A. socius* species group (Mousseau and Roff 1989*a*). Simulated daily maximum and minimum temperatures (i.e., tasmax and tasmin) were obtained for all grids within the continental United States. Only grids that were composed of at least 50% land area, based on visual inspection (number of grids = 150). All available records from 1 January 1961 to 31 December 2000 were included in the analysis.

In addition to the GFDL model cm2.0, I also examined 10 other AOGCMs: GFDL's model cm2.1, CCCMA's model cgm3.1, CNRM's model cm3, CSIRO's model mk3.0, GISS's model e20, IAP's model cm4v1, MIRCO's model v3.2, MPI's model echam5, and MRI's model cgcm2.3.2a (see Table 2 for explanation of model names). For each of these models, I randomly selected 20 grids from within the continental United States that were comprised of at least 50% land area and obtained all of the simulated daily maximum and minimum temperatures that were available from 1 January 1961 to 31 December 2000. The simulated temperatures from all of the models examined in this study represented environmental conditions two meters from the surface (Meehl et al. 2007).

For each model, grid, and year; the length of the growing season was estimated in terms of accumulated degree-days > 13°C using Allen's dual sine wave method (Allen 1976). Because I focused on the geographic scale of individual grids, downscaling methods were not employed. All of the simulated data were obtained with permission from the World Climate Research Programme's Coupled Model Intercomparison Project 3 (i.e., WCRP-CMIP3; Meehl et al. 2007). In some cases, the data files contained internal errors and could not be accessed. These data were excluded from the analysis.

Historical data

The historically observed daily maximum and minimum temperature records from 1 January 1961 to 31 December 2000 were obtained from multiple weather stations located within 1° latitude and 1° longitude of the center of each grid at standard height (1.25 m). Within the time frame, an average of 6.2 ± 0.5 (±SD) stations were available for each grid examined per year. Missing data from the historical records were replaced by that year's monthly average minimum or maximum temperature. Months in which records were missing for 15 or more days were excluded from the analysis. Years in which less than 12 months of records were available were also removed. These decisions led to an average of 36.9 ± 1.7 years being examined for each grid.

For each weather station and year, the length of the growing season was estimated in terms of accumulated degree-days > 13°C using Allen's dual sine wave method (Allen 1976). Within each grid and year, these season lengths were averaged across weather stations in order to obtain estimates of both the mean season length and its variation within a given grid. All of the historical data were obtained with permission from the National Climate Data Center (2009).

Season length analysis

For each grid and year, the simulated season length produced by a given model was compared to the mean (±SD) of the historically observed season lengths using a one-sample *t* test. A total of 5089 of these one-sample *t* tests were performed for the primary analysis (GFDL model cm2.0) and 7364 one-sample *t* tests were performed for the other models. The proportion of years in which a significant difference between the simulated and historical season lengths occurred was noted. Based on an $\alpha = 0.05$, I expected 5% of the years examined would be significant due to chance alone. Finally, the percentage difference between the simulated and historical season lengths were estimated for each grid, year, and model.

Correction factors and adjusted season lengths

The correction factors were estimated independently for each model and grid. First, the simulated daily maximum and minimum temperatures were subtracted from the average historically observed daily maximum and minimum temperatures respectively for each day in which data were available. These differences were then averaged within each year, and the results were finally averaged across years. This procedure led to a single correction factor for each of the temperature extremes that represented the average difference between the simulated and historical data across all years. Standard deviations for these estimates were also calculated and represent the across year variation in the correction factor.

These model- and grid-specific correction factors were then added to each of the simulated maximum and minimum temperatures. The simulated season lengths were recalculated, now using the adjusted maximum and minimum temperatures, and analyzed in the same manner as the unadjusted model estimations.

All statistics and calculations were performed using R (R Development Core Team 2009).

Results

Primary model

The AOGCM that was the primary focus of this study (i.e., GFDL's model cm2.0) consistently underestimated the length of the growing season across the continental United States. Across all grids and years, 0.91 ± 0.13 of the simulated season lengths were significantly different from the historical records (Table 1). On average, the simulated season lengths were 41.4% ± 18.2% less than the historical records (Table 1). The largest discrepancies between the simulated and historical season lengths were found in western Montana, Idaho, and Wyoming (Fig. 1A). In this area, the simulated season lengths were as

TABLE 1. Summary statistics for Geophysical Fluid Dynamics Laboratory (GFDL) cm2.0.

				Pr (Yrs sig)		dd diff		% diff	
Longitude	Latitude	Yrs	WS	Raw	Adj.	Raw	Adj.	Raw	Adj.
123.75	43	35	10	97.1	20.0	−411 ± 121	−54 ± 135	−46.9 ± 12.0	−5.6 ± 15.3
	41	35	14	68.6	14.3	−304 ± 113	70 ± 125	−33.0 ± 11.6	8.2 ± 14.4
121.25	47	35	10	88.6	34.3	−382 ± 137	64 ± 165	−51.1 ± 16.0	9.8 ± 22.6
	45	35	5	100.0	22.9	−524 ± 115	−100 ± 143	−62.2 ± 11.7	−11.4 ± 16.9
	43	35	14	100.0	45.7	−324 ± 117	−18 ± 136	−45.0 ± 14.0	−1.6 ± 18.9
	41	35	9	94.3	25.7	−323 ± 109	65 ± 128	−39.4 ± 11.8	8.8 ± 16.4
	39	35	10	88.6	0.0	−629 ± 147	1 ± 168	−43.2 ± 7.9	0.6 ± 11.5
	37	35	8	65.7	5.7	−488 ± 198	60 ± 210	−29.7 ± 10.2	4.7 ± 13.6
118.75	47	35	10	100.0	60.0	−779 ± 126	−139 ± 156	−68.2 ± 9.8	−11.9 ± 13.5
	45	28	10	96.4	10.7	−669 ± 115	−116 ± 143	−70.0 ± 9.3	−11.6 ± 14.7
	43	17	5	76.5	0.0	−535 ± 82	−22 ± 97	−61.3 ± 6.8	−2.1 ± 10.8
	41	20	5	100.0	20.0	−761 ± 123	−36 ± 125	−64.8 ± 6.6	−2.4 ± 10.5
	39	35	5	94.3	2.9	−796 ± 182	−31 ± 201	−62.6 ± 7.6	−0.9 ± 15.4
	37	35	22	100.0	20.0	−957 ± 202	−87 ± 228	−56.9 ± 7.1	−4.1 ± 13.0
	35	35	10	100.0	14.3	−867 ± 220	33 ± 238	−40.6 ± 7.9	2.3 ± 11.4
116.25	47	31	10	83.9	9.7	−532 ± 83	−11 ± 122	−67.1 ± 11.3	−1.5 ± 15.8
	45	35	10	100.0	17.1	−601 ± 109	−116 ± 137	−71.7 ± 9.8	−13.2 ± 15.5
	43	35	21	100.0	51.4	−829 ± 125	−62 ± 157	−71.0 ± 7.8	−4.8 ± 13.1
	41	19	4	100.0	10.5	−652 ± 119	15 ± 123	−61.6 ± 7.6	2.1 ± 11.2
	39	21	3	100.0	0.0	−657 ± 127	84 ± 152	−57.9 ± 7.6	8.3 ± 13.9
	37	34	6	97.1	11.8	−1245 ± 221	−62 ± 243	−60.5 ± 6.2	−2.1 ± 11.8
	35	31	5	45.2	0.0	−1057 ± 305	−33 ± 314	−42.7 ± 8.2	−0.2 ± 12.5
	33	35	16	88.6	5.7	−760 ± 277	−39 ± 277	−28.6 ± 8.5	−0.8 ± 10.6
113.75	47	35	10	100.0	42.9	−511 ± 92	−34 ± 122	−76.2 ± 10.3	−4.4 ± 18.3
	45	35	8	100.0	25.7	−537 ± 96	−64 ± 119	−78.1 ± 9.0	−8.4 ± 17.0
	43	35	10	100.0	42.9	−615 ± 130	10 ± 155	−66.5 ± 9.7	2.1 ± 16.3
	41	21	4	90.5	0.0	−803 ± 155	−75 ± 178	−63.8 ± 8.9	−5.3 ± 13.9
	39	35	10	100.0	45.7	−683 ± 138	45 ± 162	−55.2 ± 8.1	4.4 ± 13.5
	37	35	6	62.9	0.0	−725 ± 175	13 ± 193	−45.3 ± 8.1	1.7 ± 12.7
	35	21	6	52.4	0.0	−1348 ± 214	−156 ± 203	−48.3 ± 5.4	−5.4 ± 6.8
	33	34	5	100.0	26.5	−1452 ± 216	−146 ± 215	−40.3 ± 4.8	−3.9 ± 5.9
111.25	47	35	10	100.0	60.0	−641 ± 97	−67 ± 125	−78.5 ± 8.1	−7.5 ± 15.1
	45	35	10	100.0	5.7	−547 ± 139	−71 ± 161	−78.3 ± 9.3	−7.9 ± 20.1
	43	35	19	100.0	54.3	−413 ± 110	23 ± 132	−63.9 ± 11.8	5.1 ± 20.1
	41	35	10	100.0	20.0	−647 ± 132	70 ± 161	−61.5 ± 8.6	7.7 ± 15.6
	39	35	7	97.1	42.9	−534 ± 131	148 ± 152	−47.8 ± 8.8	14.3 ± 14.7
	37	35	13	85.7	5.7	−604 ± 180	81 ± 202	−42.2 ± 8.5	7.1 ± 14.4
	35	35	10	42.9	0.0	−467 ± 168	87 ± 177	−30.1 ± 9.6	6.2 ± 11.7
	33	35	10	100.0	2.9	−1437 ± 196	−122 ± 200	−46.1 ± 4.9	−3.7 ± 6.3
108.75	47	35	6	100.0	34.3	−624 ± 118	−86 ± 140	−70.4 ± 9.6	−8.9 ± 15.4
	45	35	10	100.0	51.4	−754 ± 106	−98 ± 135	−80.3 ± 6.2	−9.7 ± 13.4
	43	35	6	100.0	31.4	−788 ± 125	−104 ± 156	−77.7 ± 7.0	−9.4 ± 14.2
	41	34	4	100.0	5.9	−707 ± 131	22 ± 162	−65.5 ± 8.4	2.9 ± 14.8
	39	35	6	94.3	2.9	−751 ± 153	116 ± 185	−58.1 ± 8.2	10.0 ± 15.3
	37	35	21	100.0	48.6	−479 ± 130	165 ± 155	−41.6 ± 9.4	15.2 ± 14.3
	35	35	15	68.6	77.1	−203 ± 128	233 ± 142	−18.9 ± 11.5	22.8 ± 14.5
	33	35	10	45.7	8.6	−404 ± 176	147 ± 186	−25.2 ± 10.0	9.8 ± 12.1
106.25	47	35	8	100.0	82.9	−726 ± 137	−189 ± 160	−68.0 ± 9.9	−17.1 ± 13.9
	45	35	10	100.0	82.9	−708 ± 124	−126 ± 148	−72.7 ± 7.1	−11.9 ± 14.2
	43	29	4	100.0	27.6	−703 ± 130	−60 ± 171	−73.3 ± 8.2	−5.2 ± 17.0
	41	35	10	97.1	40.0	−383 ± 116	84 ± 149	−58.3 ± 13.7	14.6 ± 23.4
	39	35	10	51.4	40.0	−213 ± 134	110 ± 157	−36.8 ± 20.8	22.5 ± 29.8
	37	35	10	71.4	42.9	−272 ± 135	163 ± 161	−33.8 ± 15.7	21.5 ± 21.2
	35	35	10	74.3	34.3	−451 ± 160	213 ± 186	−34.5 ± 11.4	17.0 ± 15.3
	33	35	10	60.0	8.6	−509 ± 201	192 ± 225	−28.4 ± 10.8	11.2 ± 13.2
103.75	47	35	10	100.0	71.4	−589 ± 146	−165 ± 165	−60.8 ± 11.8	−16.3 ± 16.1
	45	35	10	100.0	54.3	−627 ± 136	−120 ± 159	−63.7 ± 9.1	−11.0 ± 16.3
	43	35	10	100.0	48.6	−688 ± 129	−110 ± 160	−64.0 ± 7.9	−9.5 ± 14.3
	41	35	10	100.0	40.0	−693 ± 169	−21 ± 207	−59.5 ± 11.6	−0.8 ± 18.2
	39	35	8	100.0	31.4	−874 ± 217	4 ± 248	−59.3 ± 12.9	0.9 ± 16.5
	37	35	7	45.7	54.3	−283 ± 258	210 ± 272	−25.1 ± 22.5	20.2 ± 25.4
	35	33	10	75.8	48.5	−546 ± 288	167 ± 306	−30.4 ± 14.8	10.1 ± 17.1
	33	33	9	66.7	33.3	−526 ± 275	104 ± 294	−23.7 ± 11.9	5.1 ± 13.5
	31	23	8	65.2	21.7	−583 ± 265	110 ± 298	−23.7 ± 10.2	4.9 ± 12.2
101.25	47	34	10	91.1	61.8	−483 ± 153	−175 ± 167	−51.9 ± 13.7	−18.2 ± 16.8
	45	35	9	91.4	54.3	−599 ± 180	−195 ± 197	−53.7 ± 12.0	−16.5 ± 16.4
	43	35	10	100.0	71.4	−704 ± 171	−164 ± 193	−55.3 ± 10.0	−12.0 ± 14.6
	41	35	10	100.0	51.4	−695 ± 184	−76 ± 208	−51.2 ± 11.1	−4.8 ± 15.3
	39	35	10	94.3	65.7	−635 ± 274	−41 ± 284	−40.7 ± 15.9	−1.8 ± 18.0

TABLE 1. Continued.

				Pr (Yrs sig)		dd diff		% diff	
Longitude	Latitude	Yrs	WS	Raw	Adj.	Raw	Adj.	Raw	Adj.
	37	35	10	88.6	71.4	−622 ± 349	−2 ± 337	−33.4 ± 17.6	0.6 ± 17.9
	35	35	10	80.0	60.0	−566 ± 350	65 ± 344	−26.3 ± 15.4	3.5 ± 15.8
	33	35	9	65.7	34.3	−431 ± 329	85 ± 338	−18.2 ± 13.3	4.1 ± 14.2
	31	35	6	80.0	42.9	−574 ± 317	56 ± 336	−20.9 ± 11.1	2.4 ± 12.4
98.75	47	35	10	100.0	74.3	−404 ± 149	−124 ± 160	−43.8 ± 14.2	−12.7 ± 17.1
	45	35	10	100.0	80.0	−531 ± 182	−162 ± 193	−46.5 ± 13.0	−13.4 ± 16.3
	43	35	10	100.0	77.1	−615 ± 199	−121 ± 215	−45.8 ± 12.2	−8.0 ± 16.3
	41	35	10	97.1	77.1	−572 ± 209	−80 ± 225	−40.3 ± 12.9	−4.7 ± 16.2
	39	35	10	97.1	71.4	−670 ± 283	−47 ± 285	−36.9 ± 14.4	−2.1 ± 15.5
	37	35	10	94.3	71.4	−629 ± 333	−5 ± 313	−29.6 ± 14.9	0.1 ± 14.4
	35	35	10	91.4	65.7	−490 ± 328	37 ± 317	−20.9 ± 13.4	1.9 ± 13.3
	33	35	10	94.3	68.6	−494 ± 326	65 ± 329	−18.7 ± 11.7	2.9 ± 12.4
	31	35	9	77.1	65.7	−411 ± 311	95 ± 319	−14.7 ± 10.9	3.7 ± 11.6
	29	33	7	87.9	45.5	−669 ± 324	66 ± 336	−20.1 ± 9.3	2.3 ± 10.3
	27	20	3	100.0	40.0	−986 ± 278	6 ± 281	−25.3 ± 7.1	0.2 ± 7.4
96.25	47	35	8	100.0	60.0	−392 ± 152	−95 ± 162	−41.3 ± 14.0	−9.1 ± 17.2
	45	35	10	100.0	82.9	−417 ± 172	−93 ± 185	−39.2 ± 14.1	−7.8 ± 17.4
	43	35	10	97.1	65.7	−499 ± 203	−88 ± 219	−39.3 ± 13.7	−5.9 ± 17.5
	41	35	10	94.3	80.0	−517 ± 226	−55 ± 239	−35.0 ± 14.1	−3.0 ± 16.4
	39	35	10	94.3	71.4	−544 ± 281	−3 ± 279	−30.0 ± 14.4	0.4 ± 15.2
	37	35	10	94.3	74.3	−426 ± 322	52 ± 310	−21.0 ± 15.1	3.2 ± 15.1
	35	35	8	88.6	68.6	−426 ± 311	99 ± 302	−18.0 ± 12.6	4.6 ± 12.6
	33	35	10	91.4	57.1	−492 ± 292	92 ± 294	−17.9 ± 10.1	3.8 ± 10.9
	31	34	10	91.2	58.8	−577 ± 264	108 ± 273	−19.2 ± 8.4	3.9 ± 9.2
	29	32	10	90.6	46.9	−577 ± 247	30 ± 258	−17.8 ± 7.4	1.1 ± 8.1
93.75	47	29	9	96.6	51.7	−359 ± 146	19 ± 158	−42.5 ± 15.0	3.6 ± 19.8
	45	35	10	97.1	60.0	−444 ± 159	−27 ± 174	−41.8 ± 13.1	−1.5 ± 17.2
	43	34	10	94.1	64.7	−441 ± 188	−30 ± 203	−36.6 ± 14.1	−1.6 ± 17.3
	41	35	10	91.4	57.1	−409 ± 244	5 ± 254	−28.9 ± 16.1	1.3 ± 18.3
	39	35	7	91.4	71.4	−456 ± 282	65 ± 281	−26.3 ± 15.2	4.4 ± 16.1
	37	35	10	82.9	71.4	−344 ± 318	123 ± 307	−17.9 ± 16.1	7.1 ± 16.2
	35	35	8	71.4	60.0	−329 ± 337	148 ± 320	−14.5 ± 14.5	7.1 ± 14.3
	33	35	10	82.9	62.9	−281 ± 274	159 ± 268	−11.0 ± 10.6	6.7 ± 10.8
	31	35	5	91.4	62.9	−376 ± 251	164 ± 256	−13.1 ± 8.7	6.0 ± 9.3
91.25	45	35	10	97.1	48.6	−417 ± 149	52 ± 167	−42.0 ± 13.1	6.4 ± 18.3
	43	35	10	94.3	54.3	−408 ± 185	25 ± 202	−35.3 ± 14.6	3.3 ± 18.4
	41	35	21	100.0	80.0	−480 ± 228	32 ± 239	−32.9 ± 14.3	2.9 ± 16.5
	39	35	10	97.1	60.0	−406 ± 269	64 ± 268	−24.5 ± 15.5	4.5 ± 16.3
	37	35	10	77.1	62.9	−347 ± 319	112 ± 303	−18.2 ± 16.6	6.4 ± 16.3
	35	35	23	88.6	80.0	−409 ± 328	114 ± 309	−17.8 ± 14.1	5.4 ± 13.8
	33	35	10	88.6	62.9	−350 ± 289	133 ± 276	−13.6 ± 11.2	5.5 ± 11.1
	31	35	10	88.6	71.4	−366 ± 268	186 ± 267	−12.7 ± 9.3	6.7 ± 9.6
88.75	45	35	10	94.3	45.7	−310 ± 146	96 ± 160	−35.0 ± 14.8	12.4 ± 19.8
	43	35	10	100.0	65.7	−398 ± 175	89 ± 195	−35.7 ± 14.5	9.1 ± 18.6
	41	35	10	97.1	68.6	−476 ± 216	51 ± 229	−33.9 ± 13.9	4.5 ± 16.6
	39	35	10	88.6	65.7	−471 ± 263	79 ± 265	−28.2 ± 15.0	5.4 ± 16.2
	37	35	9	88.6	80.0	−478 ± 298	118 ± 287	−24.7 ± 15.0	6.5 ± 15.1
	35	35	10	88.6	85.7	−453 ± 329	131 ± 309	−20.8 ± 15.0	6.4 ± 14.6
	33	35	10	77.1	68.6	−347 ± 334	146 ± 310	−14.2 ± 13.8	6.4 ± 13.2
	31	35	10	88.6	71.4	−449 ± 288	192 ± 281	−16.1 ± 10.2	7.3 ± 10.5
86.25	41	35	10	97.1	71.4	−460 ± 187	86 ± 204	−35.6 ± 13.3	7.4 ± 16.5
	39	35	10	88.6	57.1	−477 ± 226	69 ± 236	−31.2 ± 13.9	5.2 ± 15.9
	37	35	10	94.3	80.0	−537 ± 265	136 ± 262	−29.3 ± 14.0	7.7 ± 14.5
	35	35	10	88.6	77.1	−431 ± 325	131 ± 311	−22.3 ± 16.5	7.3 ± 16.6
	33	35	10	88.6	62.9	−549 ± 352	153 ± 320	−22.9 ± 14.4	6.8 ± 13.7
	31	35	9	68.6	65.7	−311 ± 317	159 ± 297	−11.5 ± 11.7	6.3 ± 11.4
83.75	45	35	10	97.1	71.4	−283 ± 126	131 ± 137	−34.7 ± 14.0	17.5 ± 18.8
	43	35	10	100.0	68.6	−486 ± 162	129 ± 184	−43.8 ± 12.5	12.9 ± 18.1
	41	35	10	97.1	65.7	−479 ± 166	66 ± 184	−39.4 ± 12.0	6.3 ± 15.8
	39	35	10	100.0	60.0	−562 ± 174	78 ± 191	−38.1 ± 10.7	5.7 ± 13.3
	37	35	10	100.0	74.3	−624 ± 201	136 ± 211	−38.0 ± 11.7	8.5 ± 13.0
	35	35	10	77.1	48.6	−404 ± 250	218 ± 247	−24.4 ± 14.8	13.4 ± 15.1
	33	35	10	94.3	57.1	−704 ± 314	173 ± 288	−29.2 ± 12.6	7.5 ± 12.3
	31	35	10	91.4	65.7	−581 ± 335	152 ± 310	−20.2 ± 11.4	5.5 ± 11.0
81.25	41	35	9	100.0	48.6	−553 ± 133	109 ± 158	−47.4 ± 9.5	10.1 ± 14.4
	39	35	9	100.0	42.9	−687 ± 145	92 ± 163	−47.9 ± 8.4	6.9 ± 11.8
	37	35	10	91.4	37.1	−437 ± 164	147 ± 180	−33.2 ± 11.7	11.6 ± 14.0
	35	35	9	97.1	37.1	−697 ± 206	185 ± 208	−36.3 ± 10.2	9.9 ± 11.1
	33	35	10	100.0	62.9	−654 ± 263	147 ± 244	−26.0 ± 10.1	6.1 ± 10.0

TABLE 1. Continued.

Longitude	Latitude	Yrs	WS	Pr (Yrs sig) Raw	Pr (Yrs sig) Adj.	dd diff Raw	dd diff Adj.	% diff Raw	% diff Adj.
	27	35	20	97.1	74.3	−568 ± 190	26 ± 190	−15.1 ± 4.8	0.8 ± 5.1
78.75	41	35	10	100.0	37.1	−472 ± 111	78 ± 134	−48.6 ± 9.5	8.8 ± 14.5
	39	35	10	97.1	22.9	−544 ± 137	119 ± 155	−43.3 ± 9.3	10.1 ± 13.1
	37	35	10	100.0	57.1	−754 ± 153	147 ± 171	−42.9 ± 7.9	8.6 ± 9.9
	35	35	10	100.0	54.3	−797 ± 191	160 ± 192	−36.3 ± 8.0	7.5 ± 8.9
76.25	41	35	6	94.3	17.1	−554 ± 132	74 ± 159	−51.0 ± 9.4	7.8 ± 15.5
	39	35	10	100.0	71.4	−821 ± 143	153 ± 168	−49.2 ± 7.1	9.6 ± 10.6
	37	34	6	79.4	5.9	−822 ± 230	58 ± 231	−39.7 ± 8.7	3.7 ± 12.0
73.75	43	35	9	100.0	22.9	−552 ± 113	−37 ± 137	−61.1 ± 8.8	−3.2 ± 15.2
	41	35	10	100.0	37.1	−643 ± 138	−52 ± 162	−52.4 ± 8.8	−3.6 ± 13.4
71.75	43	35	10	100.0	48.6	−573 ± 111	−60 ± 134	−61.3 ± 8.6	−5.7 ± 14.1
68.75	45	35	5	100.0	31.4	−553 ± 88	−77 ± 111	−72.2 ± 7.0	−9.2 ± 14.3
Mean		34	9.6	90.6	46.6	−569 ± 207	32 ± 103	−41.4 ± 18.2	2.1 ± 8.2

Notes: Grids are organized by longitude (°W) and latitude (°N). Sample sizes are broken down into the number of years (Yrs) examined and the average number of weather stations per year (WS). Pr (Yrs sig) represents the proportion of years in which a significant difference in season length was detected. Accuracy is represented by the difference between the model and historical records in terms of degree-days (dd diff) and percentages. These statistics were calculated using the model's Raw and adjusted (Adj.) output. Values shown are means ± SD.

much as 80% less than the historical observations (see 45° N, 108.75° W; Table 1). The model performed best in the deep south (Fig. 1A). But even in this region, the simulated season lengths were at least 11% lower than the historical observations (see 33° N, 91.25° W; Table 1).

Not surprisingly, the GFDL model cm2.0 also underestimated both the daily maximum and minimum temperatures. However, the magnitude of this underestimation was greater for the daily maximum temperatures. When averaged across all grids, the maximum temperatures were underestimated by 5.9°C ± 1.9°C, while the daily minimum temperatures were underestimated by only 2.6°C ± 1.6°C (Table 2). The largest differences in daily maximum temperature estimates were generally found in the northwestern quarter of the country with the exception of a few regions along the east coast (Fig. 2A). In contrast, the largest differences for the minimum temperatures were found primarily in the southwestern portion of the country (Fig. 2B).

After using the grid-specific correction factors (Table 1) to adjust the simulated daily maximum and minimum temperatures (see *Methods*), the accuracy of the model's simulated season lengths improved. The proportion of season lengths across all years and grids in which significant differences were detected was cut nearly in half from 0.91 before the adjustments to 0.47 after the adjustments were applied (Table 1). In addition, the average difference in season length estimates went from an underestimation of 41.4% ± 18.2% to an overestimation of 2.1% ± 8.2% (Table 1). The adjusted season lengths were closest to the historical season lengths in the central portion of the United States and along the west coast (Fig. 1B). In addition to improving the accuracy of the simulated season lengths, the correction factors also significantly reduced the variation in accuracy across grids (Fig. 3). The standard deviation of the model's accuracy was 18.2% before the adjustment, but only 8.2% after the adjustment was applied ($F_{149,149} = 10.0$, $P < 0.0001$).

Cross model comparisons.—Substantial variation in the ability to accurately simulate season lengths was observed across all of the AOGCMs examined in this

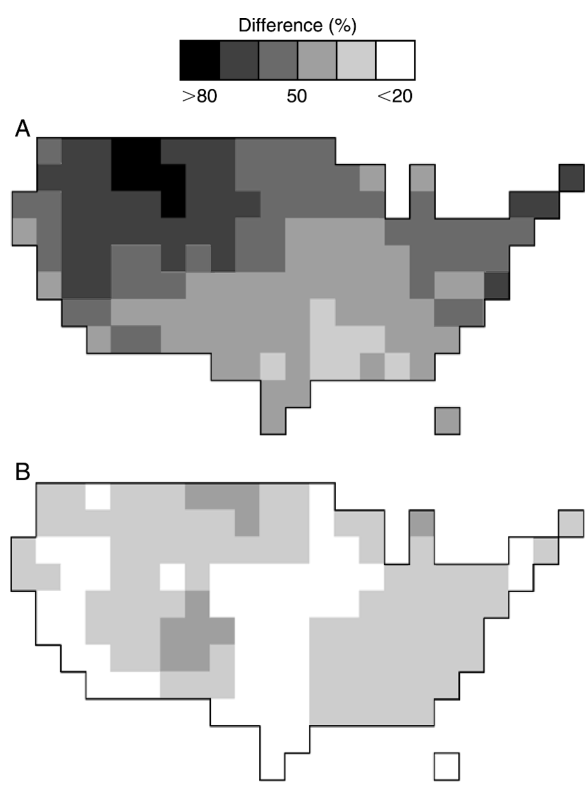

FIG. 1. The absolute percentage difference between the simulated and historical season lengths averaged across all years from 1961 to 2000 for the Geophysical Fluid Dynamics Laboratory (GFDL) model cm2.0 using (A) raw model output and (B) adjusted model output.

TABLE 2. The summary statistics for 11 atmosphere and ocean general circulating models (AOGCMs) examined in this study.

Model	Sample size			Pr (Yrs sig)		Corr. factors (°C)	
	Gds	Yrs/Gds	WS/Yr	Raw	Adj.	Tmax	Tmin
GISS	20	38.5 ± 3.4	6.8 ± 3.6	0.84 ± 0.21	0.59 ± 0.30	−3.6 ± 3.0	2.2 ± 1.7
GFDL 2.0	150	33.6 ± 4.1	6.4 ± 2.7	0.91 ± 0.13	0.47 ± 0.25	−5.9 ± 1.4	−2.6 ± 1.0
GFDL 2.1	20	39.3 ± 3.4	6.1 ± 1.6	0.83 ± 0.65	0.49 ± 0.22	−5.3 ± 1.8	−1.9 ± 1.9
CSIRO	20	34.8 ± 9.0	6.0 ± 2.8	0.65 ± 0.33	0.30 ± 0.28	−4.2 ± 2.6	0.1 ± 2.3
IPSL	19	37.0 ± 3.4	5.5 ± 1.6	0.71 ± 0.24	0.41 ± 0.23	−4.6 ± 2.3	0.7 ± 2.0
MPI	20	36.9 ± 7.8	6.3 ± 2.7	0.67 ± 0.28	0.34 ± 0.27	−2.7 ± 2.6	2.1 ± 2.5
CCCMA	20	37.3 ± 6.8	5.5 ± 1.5	0.63 ± 0.26	0.41 ± 0.27	−1.7 ± 2.8	−1.4 ± 2.1
CNRM	20	38.1 ± 4.0	5.7 ± 1.6	0.65 ± 0.34	0.38 ± 0.30	−3.0 ± 1.7	0.4 ± 2.2
MRI	20	37.3 ± 6.9	6.2 ± 2.3	0.60 ± 0.27	0.43 ± 0.24	−1.5 ± 1.9	0.1 ± 1.5
IAP	20	37.1 ± 8.6	6.5 ± 1.9	0.59 ± 0.31	0.33 ± 0.28	−2.1 ± 2.4	0.8 ± 2.1
MIROC	19	35.5 ± 9.4	7.0 ± 3.5	0.68 ± 0.32	0.39 ± 0.26	−1.9 ± 3.1	3.6 ± 1.7
Overall		36.9 ± 1.7	6.2 ± 0.5	0.71 ± 0.11	0.41 ± 0.08	−3.3 ± 1.5	0.4 ± 1.9

Notes: Sample sizes are broken down into the number of grids examined (Gds), the average number of years available per grid (Yrs/Gds), and the average number of weather stations per year within each grid (WS/Yr). The proportion of years in which the simulated season length differed significantly from the historical observation, Pr (Yrs sig), is presented both before the correction factors were included (Raw) and after (Adj.). Average correction factors (Corr. factors) for both maximum (Tmax) and minimum (Tmin) temperatures are also reported. Values are means (±SD) across grids, with the exception of the overall row which is the mean across all models (±SD). Models are GISS, Goddard Institute for Space Studies; GFDL, Geophysical Fluid Dynamics Laboratory; CSIRO, Commonwealth Scientific and Industrial Research Organization; IPSL, Institut Pierre Simon Laplace; MPI, Max Planck Institute for Meteorology; CCCMA, Canadian Centre for Climate Modeling and Analysis; CNRM, Centre National de Recherches Meteorologiqye; MRI, Meterological Research Institute; IAP, Institute of Atmospheric Physics; MIRCO, Model for Interdisciplinary Research on Climate.

study (Fig. 4). The GISS model was the least accurate, and on average underestimated the season length by 44.3% ± 26.8%. The IAP and MIRCO models were the most accurate, overestimating the season length by an average of 1.2% ± 32.6% and 3.5% ± 29.4%, respectively. These were the only two models in which the simulated season lengths based on the models' raw data were not significantly different from the historical observations (IAP, $t_{19} = 0.16$, $P = 0.8710$; MIRCO, $t_{19} =$

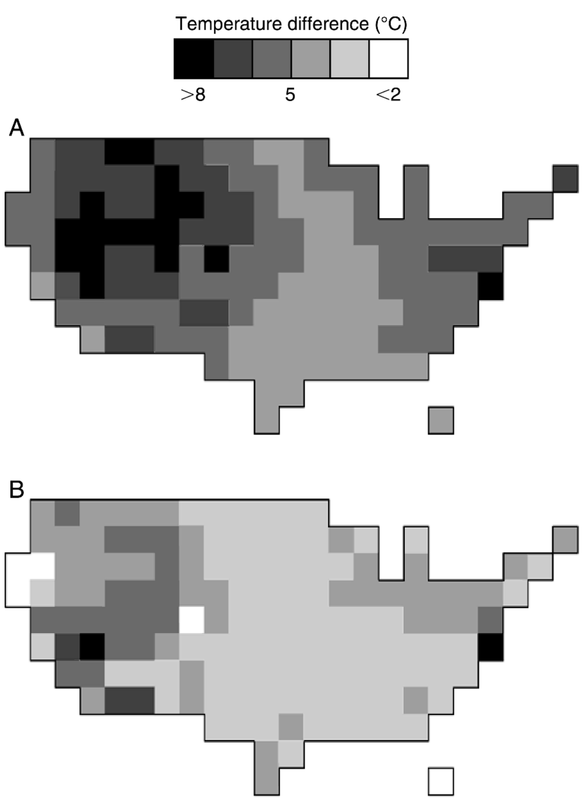

FIG. 2. The absolute difference between the simulated and historical daily (A) maximum and (B) minimum temperatures for the GFDL model cm2.0 averaged across all days from 1 January 1961 to 31 December 2000.

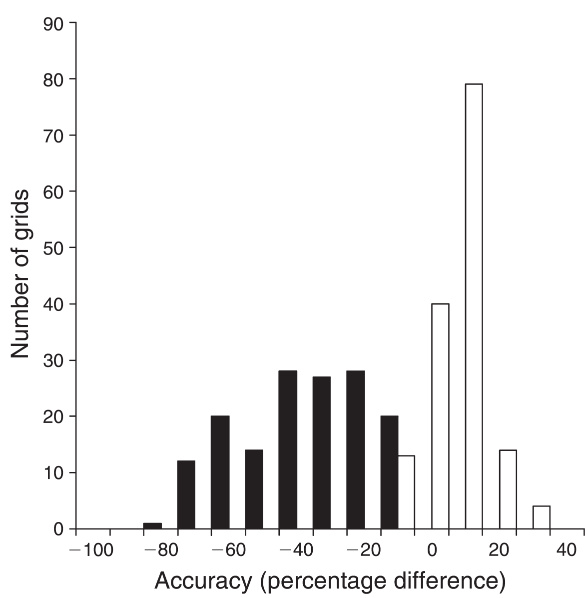

FIG. 3. The percentage differences between the simulated and historical season lengths across all grids examined in the GFDL model cm2.0 using raw model output (dark bars) and adjusted output (light bars).

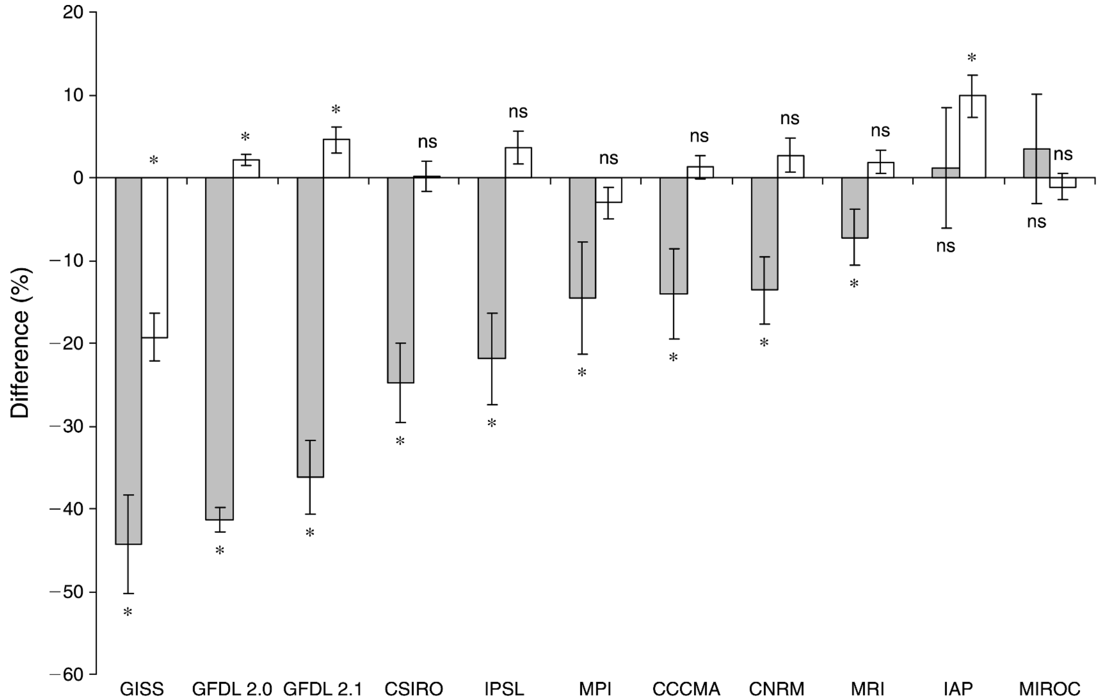

FIG. 4. The percentage differences between the simulated and historical season lengths for all 11 atmosphere and ocean general circulating models (AOGCMs) examined in this study using raw data (dark bars) and adjusted data (light bars). Each estimate is the average across both grids and years (±SE). Significance tests based on a one-sample *t* test for each model are summarized below the zero line for the raw output and above the zero line for the adjusted output.
* $P \leq 0.05$; ns, not significant.

0.53, $P = 0.6006$). All of the other models examined significantly underestimated the historical season lengths across grids ($\alpha = 0.05$).

Generally after the correction factors were added to the models' output, the accuracy of the simulated season lengths was improved. For most models, the average difference between the simulated and historical season lengths decreased after the correction factors were applied (Fig. 4). Across all models, the difference between the simulated and historical season lengths went from an underestimation of 18.6% ± 4.5% prior to the correction factors being applied to an overestimation of 1.2% ± 6.7% afterward. In addition, the proportion of years in which a significant difference was detected between the simulated and historical season lengths decreased for all models (Table 2). Before the correction factors were applied, 0.71 ± 0.11 of the simulated season lengths were significantly different from the historical records (averaged across all models), but only 0.41 ± 0.08 were significantly different afterward (Table 2). This difference represented a significant improvement in the models' ability to simulate historical season lengths ($t_{20} = 7.4$, $P < 0.0001$).

Despite the fact that the adjusted season lengths were generally more accurate than the unadjusted estimates, significant differences between the adjusted and historical season lengths were still detected in four of the 11 models examined (Fig. 4). In two of these four models (GFDL 2.0 and GFDL 2.1), the differences were relatively small, and in the case of the GFDL 2.0 model's the statistical power was quite large (number of grids = 150). The accuracy of the GISS model was improved after the correction factors were applied (Fig. 4), although the simulated season lengths were still 19.3% ± 12.9% lower than the historical observations. In contrast, the accuracy of the IAP model actually decreased after the correction factors were applied (Fig. 4). Prior to the adjustment, the season length estimate in the average grid of the IAP model was 1.2% greater than the historical observation, while after the adjustment it was 9.9% greater. However, the variation in accuracy of this model across grids did decrease significantly after the correction factors were applied. The standard deviation before the adjustment was 32.6%, but only 11.4% afterward ($F_{19,19} = 2.86$, $P = 0.0135$).

DISCUSSION

Although the general inability of AOGCMs to simulate historical season lengths at the regional geographic scale was expected, the amount and levels of variation were surprising. In this study, the accuracy of the season length predictions varied both geographically (Fig. 1A), as well as across models (Fig. 4).

One potential explanation for the geographic variation observed in this study involves the number of weather stations within each grid that were available for analysis. Of the 150 grids examined in the primary model, 46 had fewer than 10 weather stations (Table 1). Within this subgroup, sample size had a significant effect on the accuracy of the simulated season length ($F_{1,45} = 8.5$, $P = 0.006$, $r^2 = 0.16$). For each additional weather station, the accuracy of the simulated season lengths increased by an average of 4.2% ± 1.4% (mean ± SE). However, this sample size effect was not present for grids that had 10 or more weather stations available ($F_{1,101} < 0.1$, $P = 0.995$, $r^2 < 0.01$). In addition, the grids that exhibited the greatest discrepancies between the simulated and historical season lengths (i.e., Montana, Wyoming, Idaho; Fig. 1A) had an average of 10.4 ± 1.5 (mean ± SE) weather stations. This relatively large sample size in an area of low accuracy suggests that sample size alone was not the sole cause of the inaccuracies found in Montana, Wyoming, and Idaho. The most likely explanation for these inaccuracies is the low spatial resolution of AOGCMs at higher altitudes. This lack of spatial resolution has been found to underestimate albedo feedback and daily high temperatures (Christensen et al. 2007), which in turn would lead to the large underestimation of season length found in this study. Thus, geographic variation in the ability of AOGCMs to simulate historical season lengths appears to be due, in part, to their spatial resolutions. As such, I would thus expect geographic variation to be lower for climate models with higher spatial resolutions. These mesoscale climate models may be better than AOGCMs in predicting how biological populations will respond to climate change, particularly if research interests are confined to a specific area or region. Furthermore, as AOGCMs are improved and refined, I expect the geographic variation in their accuracy to decrease as well.

Unlike the geographic variation observed within the primary model, variation across AOGCMs did not appear to be related to their spatial resolutions. The relationship between grid size and the accuracy of the simulated season length across models was not significant ($F_{1,9} = 0.4$, $P = 0.536$, $r^2 = 0.04$). This result was not surprising given that the AOGCMs used in this study had similar spatial resolutions. On average, grids were 2.6° ± 0.3° in longitude and 2.3° ± 0.3° in latitude (mean ± SE). The inter-model variation observed in this study is most likely caused by differences in the mathematical composition of the AOGCMs, particularly how cloud feedback is incorporated (Randall et al. 2007). This inter-model variation is likely to persist as different research groups employ alternate strategies to optimize mathematical complexity, simulation run time and parameterization.

The variation observed across both geographic areas and separate AOGCMs emphasize the fact that no universal set of correction factors will consistently improve the predictions of all AOGCMs. As such, the most appropriate set of correction factors for a given study will be dependent on its specific goals, particularly on the geographic areas of interest and the specific AOGCM being used.

Despite the large amounts of variation observed in the raw AOGCMs season length simulations, most models consistently underestimated historical season lengths. This underestimation of season length appears to be driven primarily by the model's underestimation of daily maximum temperatures. The geographic distribution of season length discrepancies (Fig. 1A) and daily maximum temperature correction factors (Fig. 2A) were not only closely associated, but the correlation between accuracy and the daily maximum correction factor across models (Table 2) was also significantly positive ($r = 0.811$, $t_{10} = 4.2$, $P = 0.0025$). In contrast, the distribution of daily minimum correction factors (Fig. 2B) and season lengths discrepancies (Fig. 1) did not appear to be strongly associated, while the correlation of accuracy and daily minimum correction factors across models was positive, but not significant (Table 2; $r = 0.458$, $t_{10} = 1.5$, $P = 0.1564$).

The stronger association between daily maximum temperatures and season length estimates should be expected, given that for a large portion of the year, daily minimum temperatures will fall below the lower thermal threshold for development of the focal species (i.e., 13°C). As such, underestimations of the daily minimum temperatures will not contribute to the accumulation of degree-days during these portions of the year. In contrast, daily maximum temperatures will frequently be within the focal organism's upper (35°C) and lower (13°C) thermal thresholds for growth. Because of this relationship, any consistent underestimation in simulated daily high temperatures will lead to an underestimation of accumulated degree-days (i.e., season length).

Because the season length estimates of temperate ectotherms are dependent on both the daily maximum and minimum temperatures, and the upper and lower thermal thresholds for development of the focal organism; the accuracy of simulated season lengths may vary across species. Organisms with a lower thermal threshold substantially below 13°C should be more sensitive to underestimations of daily low temperatures than *A. socius* species group. This increased sensitivity would be due to the fact that more of the observed daily minimum temperatures would fall within the organism's usable thermal range. Likewise, organisms with an upper thermal threshold substantially higher than 35°C should be more sensitive to underestimations of daily maximum temperatures than the *A. socius* species group, because a higher proportion of the daily maximum temperatures would fall within their usable thermal range.

Interestingly, regardless of the upper and lower thermal thresholds of a particular organism, the correction factors used to improve the accuracy of the simulated season lengths would be the same. Because the estimation of the correction factors are based only on the differences between the simulated and historical maximum and minimum temperatures, and do not take into consideration the organism's thermal thresholds, the grid-specific correction factors estimated here (Table 1) could be used for any ectothermic organism residing within the continental United States. However, because the models simulated daily maximum and minimum temperatures are "near surface," meaning that they approximate air temperatures 2 m above the ground (Meehl et al. 2007), they do not necessarily represent the range of temperature microhabitats available to organisms within an area (Sinclair et al. 2003, Inouye 2008). Organisms capable of selecting microhabitats within a particular region may not respond as predicted by any climate simulation. As such, population level predictions based on either raw or corrected model data should be interpreted with caution.

Perhaps the most interesting observation of this study was the large amount of variation in the ability of the correction factors to improve the accuracy of the simulated season lengths. The average difference between the simulated season lengths after the correction factors were applied and the historical observations varied both geographically (Fig. 1B) and across models (Fig. 4). Although this variation in the effectiveness of region specific correction factors is likely to exist for all environmental parameters; it has not been previously reported, and it is not typically included in studies of the impact of global climate change on biological populations. Usually in these studies, the manner in which region specific correction factors were obtained is outlined in the methods section without any evaluation of their effectiveness. The implicit assumption of these studies is that the correction factors adequately remove potential discrepancies between the simulated and historical environmental parameters. However, the results of this study demonstrated that even after the application of correction factors, average simulated environmental parameters can still be off by as much as 19.3% (GISS, Fig. 4). Therefore, the effectiveness of region specific correction factors should be explicitly considered and reported in future studies of global climate change impacts on biological populations.

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