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Insignificant Change in Antarctic Snowfall Since the International Geophysical Year

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of certain natural heuristics. These include choosing colors that will result in the fewest local conflicts (mentioned on 11 surveys), as well as attempting to avoid conflicts with neighbors with high connectivity (mentioned on 39 surveys, and obviously applicable to only those two information views that revealed such neighboring information), presumably on the logic that highly connected vertices present the most constrained and difficult problems for subjects. Surveys and the experimental data also revealed a number of instances of signaling behavior by subjects, but here there was less consistency. Some subjects clearly alternated between two colors that were unused in their neighborhood in an attempt to inform neighbors of this fact. Others would alternate between colors in an attempt to call attention to conflicts. Although such signaling behaviors are apparent in the data, it is unclear whether they ever had their intended effects. Many subjects also reported introducing conflicts into their local neighborhood even when they had an available color, in an attempt to perturb the global state from a perceived stasis or local minimum. Even excluding perturbations introduced 2 s or less after the absence of any local conflicts (to account for reaction time), the 38 experiments together had 181 such incidents. This behavior might be viewed as a human analog of the deliberate injection of randomization or "thermal noise" into common optimization algorithms such as simulated annealing. Further work is needed to integrate these observations with statistical methods applied to the experimental data, in order to develop plausible stochastic models of individual behavior in the coloring problem. Ideally such models, when run in multiple independent copies, could predict which networks would be easy or difficult for human populations.

Although the results presented here are suggestive, they are limited in a variety of important ways. The human subject networks were small, a perhaps necessary consequence of the carefully controlled, simultaneous play experiments. It is tempting to contemplate Web-based studies (*25*) on a much larger scale, which will require addressing incentives, attrition, communication, and many other issues. The network topologies examined here were but a sampling of the rich space of possibilities and recent network formation models. Rather than imposing a chosen network structure on subjects, it would also be interesting to consider scenarios in which the subjects themselves participated in the network formation process, while still allowing some variability of structure. Future work should consider an even wider range of natural collective problems and activities. Candidates include problems of agreement or consensus rather than differentiation, and problems involving the formation of local teams or subgroups specifying certain properties (such as being fully connected or having at least one member of each of a fixed number of types or roles).

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Insignificant Change in Antarctic Snowfall Since the International Geophysical Year

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Antarctic snowfall exhibits substantial variability over a range of time scales, with consequent impacts on global sea level and the mass balance of the ice sheets. To assess how snowfall has affected the thickness of the ice sheets in Antarctica and to provide an extended perspective, we derived a 50-year time series of snowfall accumulation over the continent by combining model simulations and observations primarily from ice cores. There has been no statistically significant change in snowfall since the 1950s, indicating that Antarctic precipitation is not mitigating global sea level rise as expected, despite recent winter warming of the overlying atmosphere.

Global sea level (GSL) has been increasing by 1.7 mm year^{-1} over the past century (*1*) and 2.8 mm year^{-1} over the past decade (*2*). One of the greatest uncertainties in predictions of GSL rise is the contribution of the Antarctic ice sheets (*3*). The Antarctic ice budget is balanced by the buildup of snowfall in the interior and wastage due to

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melting and calving of ice along the coastal margins. Future scenarios from global climate models (GCMs) suggest that Antarctic snowfall should increase in a warming climate, mainly due to the greater moisture-holding capacity of warmer air (*4*), partially offsetting enhanced loss at the ice sheet peripheries. Perplexing temperature trends have been reported over Antarctica since continuous monitoring began with the International Geophysical Year (IGY) in 1957–1958, varying by the season, the region, and the time period analyzed (*5*, *6*). A recent study suggests a strong tropospheric warming signal has been manifested over Antarctica during winters since the early 1970s (*7*), the season during which much of the continent receives its maximum snowfall (*8*). Satellite-based ice velocity and altimetry measurements indicate that the West Antarctic Ice Sheet (WAIS) has been thinning over the past decade, with a contribution to GSL rise of 0.13 to 0.16 mm year^{-1} (*9*, *10*), consistent with widespread melting of ice sheet grounding lines (*11*). In light of these studies, it is essential to assess whether Antarctic snowfall has been increasing.

The latest studies using global and regional atmospheric models to evaluate changes in Antarctic snowfall indicate that no statistically significant increase has occurred since ~1980 over the entire grounded ice sheet, WAIS, or the East Antarctic Ice Sheet (EAIS) (*12*–*14*). A validation of the modeled-versus-observed changes (*12*) suggested that the recent model records are more reliable than the earlier global model records that inferred an upward trend in Antarctic snowfall since 1979 (*15*). The new studies also showed that interannual snowfall variability is considerable; yearly snowfall fluctuations of ±20 mm year^{-1} water equivalent (WEQ), i.e., ±0.69 mm year^{-1} GSL equivalent, are common (*12*) and might easily mask underlying trends over the short record. It is necessary to extend the snowfall record back to the IGY so that (i) trends can be assessed within a longer context, (ii) the snowfall record can be compared with the entire instrumental temperature record over Antarctica, and (iii) a 50-year benchmark for GCM evaluation is available.

The small volume of meteorological data over the Southern Ocean and Antarctica renders modeled snowfall amounts highly questionable before the modern satellite era (~1979) (*13*, *16*). The only other records of snowfall variability before 1979 are from ice cores, snow pits, and precipitation gauges. The spatial coverage of these data has been too sparse to accurately assess snowfall accumulation over the entire continent. However, in recent years scores of new ice core records have become available, due in large part to the International Transantarctic Scientific Expedition (ITASE), a multinational field program aimed at reconstructing the recent climate history of Antarctica through ice coring and related observations along an extensive network of traverses (*17*). In this study, we used these new records together with existing ice cores, snow pit and snow stake data, meteorological observations, and validated model fields to reconstruct Antarctic snowfall accumulation over the past 5 decades.

Each observational record is representative of an area surrounding it (a "zone"), the size of which depends on the atmospheric circulation, the interaction of wind with topography, and the time scale considered. Our method used meteorological model reanalysis fields to determine zones of snowfall coherence that correlate with the individual records at annual time scales. Assuming these zones adequately cover most of the continent given the available observational records, this information can be used to synthesize the observations into a continent-wide record of snowfall accumulation in a self-consistent manner. The model reanalysis data set we used is the European Centre for Medium-Range Weather Forecasts 40-Year Reanalysis (ERA-40) (*18*). We defined snowfall accumulation from ERA-40 precipitation fields that were adjusted to match long-term observed accumulation records (*19*). Precipitation dominates snowfall accumulation variability over Antarctica at model grid scales (*8*, *15*). ERA-40 precipitation was compared to independent observed accumulation records for overlap periods and shown to largely reproduce the interannual snowfall accumulation variability and

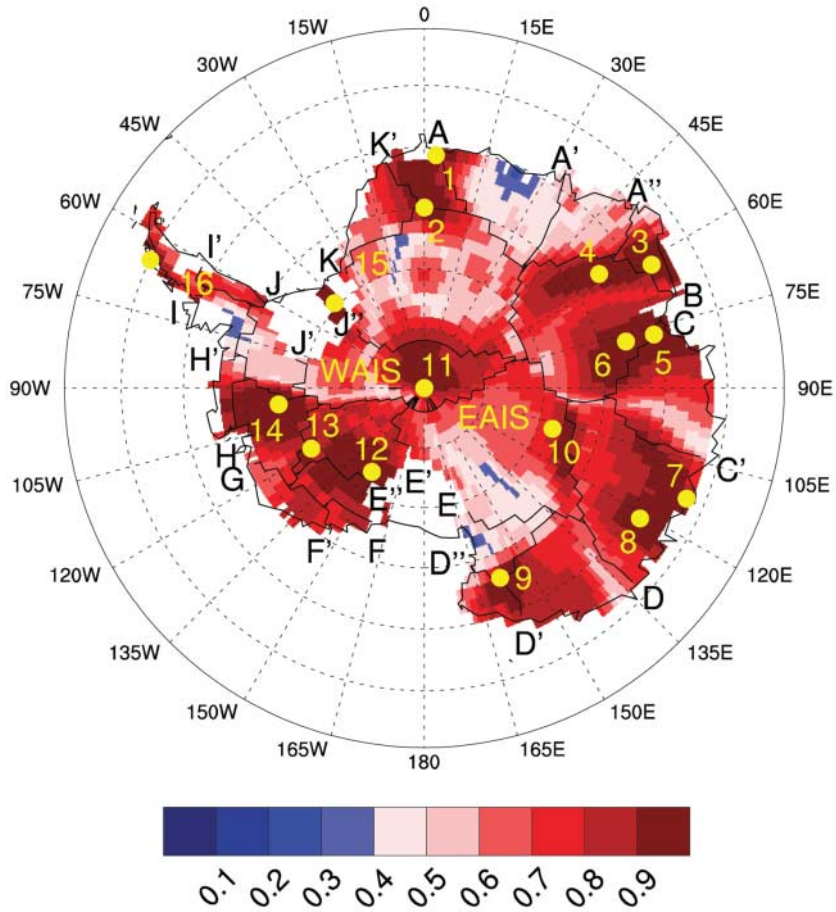

Fig. 1. The composite map of the maximum absolute value of the Pearson's correlation coefficient ($|r|$) resulting from correlating the ERA-40 1985–2004 percentage annual snowfall accumulation change (with respect to the 1985–1994 mean) for the grid box containing each of the 16 observation sites (yellow dots and numbers) with every other 1°-by-1° grid box over Antarctica (i.e., this map is a composite of 16 maps). Pink and red colors have correlations at $P < 0.01$. The black lines delineate ice drainage basins (*20*), which are identified alphabetically by the black letters where they intersect the grounding line. Detailed information about the observation sites is included in (*19*).

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trends, justifying its use for this study (*19*). Figure 1 shows a composite map of the maximum correlation coefficient obtained by correlating the ERA-40 simulated percentage annual precipitation anomaly at the grid point closest to each core with every other grid point. Correlations greater than 0.5 ($P < 0.01$) occur over most of the grounded ice sheet, indicating that the zones of spatial coherence from the available observational records cover nearly the entire continent. We used this robust relationship to synthesize the observational data into a series of continent-wide snowfall accumulation maps for the period before 1985, when the precipitation variability simulated by ERA-40 is questionable (*12*). The result is a 5-decade time series of snowfall accumulation over the grounded ice sheet; the first 3 decades are inferred from observational records, and the final 2 decades from ERA-40. A detailed description of the methodology is given in (*19*).

The spatial distribution of the 50-year average annual snowfall accumulation (Fig. 2A) closely resembles the glaciological estimate of Vaughan *et al*. (*20*). The mean for the grounded ice sheet is 182 mm year^{-1} WEQ, larger than the value of 149 mm year^{-1} WEQ from the Vaughan map. A subsequent analysis (*21*) suggested that the Vaughan map underestimated coastal accumulation and that a more realistic estimate is 171 mm year^{-1} WEQ. Overall, our mean annual snowfall accumulation is at the high end of published estimates [119 to 197 mm year^{-1} WEQ (*13*, *22*)] but may be realistic in light of recent findings.

The percentage differences of annual snowfall accumulation for each decade with respect to the 50-year mean (Fig. 2A) are shown in Fig. 2, B to F. There are regions of both positive and negative change in all 5 decades, but no continental-scale changes of either sign dominate any period. The amplitude of the changes in Fig. 2, B to D, the decades reconstructed from ice cores, is slightly dampened compared with the final two decades (Fig. 2, E and F). This is partly due the reconstructed data having smaller interannual variability than the model data; however, this does not affect the sign of the changes and has little impact on the results at basin and continental scales (*19*). There is no widespread signal of increased snowfall accumulation over the EAIS for 1995–2004 that would suggest a contribution to the recently reported thickening (*23*). The 1995–2004 changes are mostly negative over WAIS, where net ice sheet thinning is occurring (*9*, *10*). The statistical uncertainty associated with the change at each grid point (due to the decadal variability and methodology) is typically about 4 to 8%, enough to overwhelm the decadal changes in most places.

The time series of snowfall accumulation inferred from Fig. 2, B to F, and averaged over EAIS, WAIS, and the entire grounded ice sheet is shown in Fig. 3. All three regions are characterized by a steady upward trend from the beginning of the record through the early 1990s and then a downward trend thereafter that is most marked over WAIS (22 mm year^{-1} WEQ for the past decade compared with the prior decade). However, this change has low statistical significance ($P = 0.16$), indicating that decadal fluctuations of this magnitude (~7% of the 50-year mean) are probably common over WAIS. The upward trend over the ice sheets

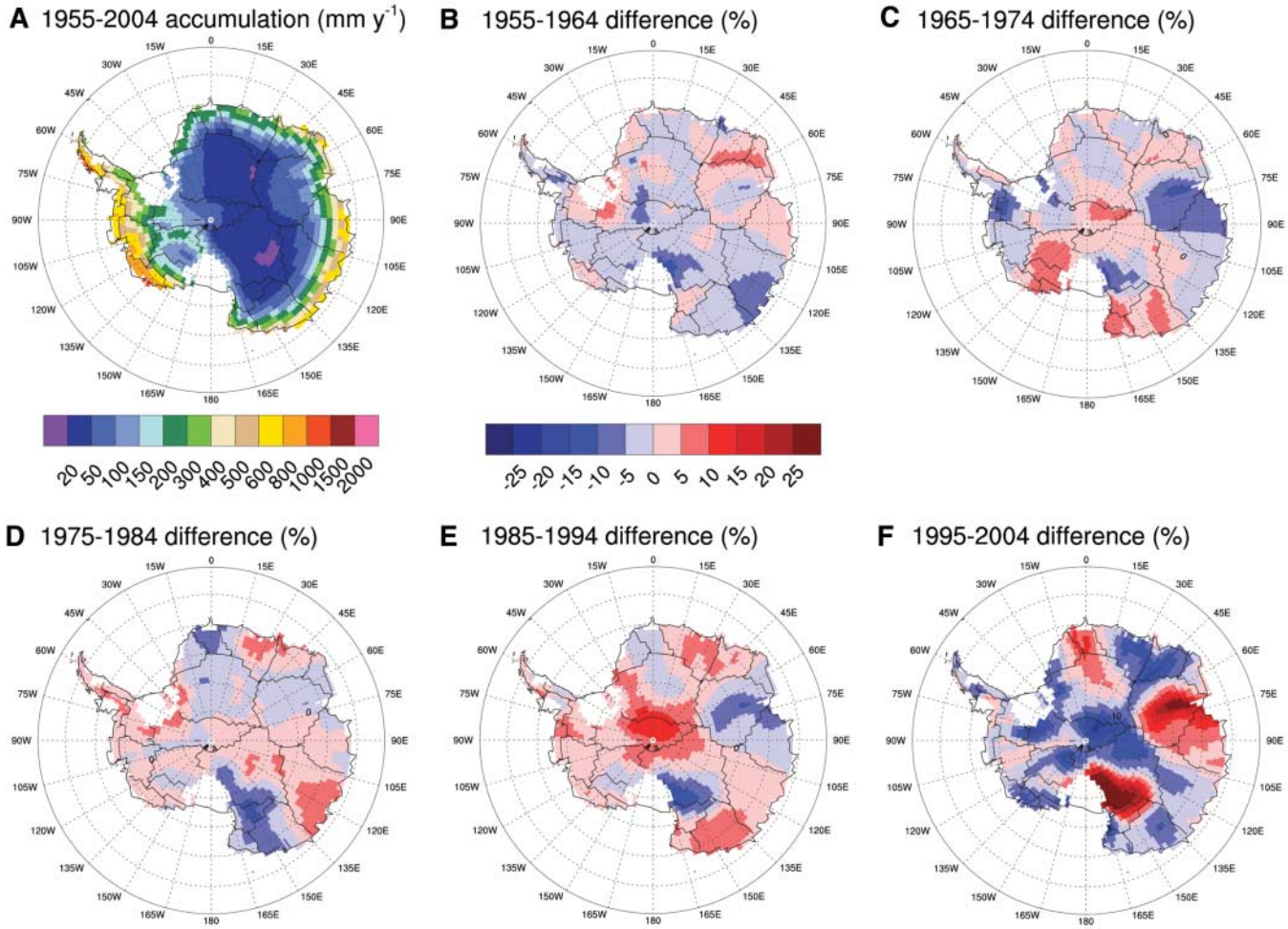

Fig. 2. (**A**) 50-year mean annual snowfall accumulation (mm year^{-1} WEQ). (**B** to **F**) Differences between mean annual snowfall accumulation for decade indicated and 50-year mean, expressed as a percentage of the 50-year mean. The scale shown in (B) applies to (B) to (F). The mean accumulation, trends, and uncertainty are quantified for each basin in (*19*).

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before the most recent decade corroborates earlier studies that used regional records (*24*, *25*). Over EAIS, WAIS, and the grounded ice sheet, there are no statistically significant trends in snowfall accumulation over the past 5 decades, including recent years for which global mean temperatures have been warmest (*26*). We performed several experiments to test the sensitivity of the results in Fig. 3 by adjusting parameters within our methodology and by using other methods to reconstruct the accumulation, and the results were very robust (*19*).

Our findings are somewhat inconsistent with Davis *et al*. (*23*), who inferred from satellite altimetry data that an increase in snowfall accumulation was the primary cause of net thickening over EAIS for 1992–2003. One reason for the discrepancy may be that their radar data did not extend southward of 81.6°S, a region with strong downward trends in the past decade (Fig. 2F). Another factor may be their methodology. Zwally *et al*. (*10*) found a thickening over EAIS from satellite altimetry for a similar period that was a factor of 3 smaller than the value from the Davis study, arguing that their method more accurately accounts for firn compaction and interannual variability of the surface height. Lastly, because snowfall typically adjusts to climate change on much shorter time scales than the underlying glacial ice (*27*), a linear thickening trend as reported in the Davis study could be interpreted to mean that snowfall accumulation from 1992–2003 was stepwise higher than at some time in the past, when the accumulation rate and the ice sheet dynamical response were in equilibrium. In that case, the results of Davis *et al*. (*23*) may actually suggest that snowfall accumulation over EAIS has changed little in the past decade, consistent with our assessment. Despite our disagreement as to the causality, we do not dispute that altimetry indicates a clear thickening signal over EAIS (*10*, *23*) that mitigates sea level rise.

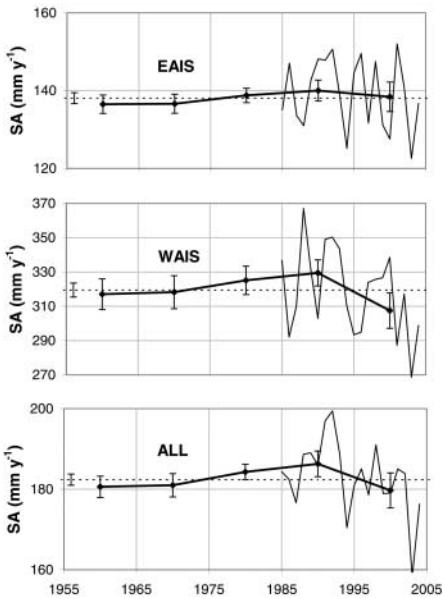

Fig. 3. Time series of decadal mean of annual snowfall accumulation (mm year^{-1} WEQ) for 1955–2004 for EAIS, WAIS, and the grounded ice sheet (ALL), calculated as described in the text. The annual accumulation is also shown for the past 2 decades, the period for which ERA-40 is used. The dotted line represents the 50-year mean. The basins that define EAIS, WAIS, and ALL are given in (*19*). Uncertainty bars are ±1σ per our methodology (*19*). The uncertainty bar at the far left of each graph is for the 50-year mean.

The implications of our findings are categorized into two general ideas.

1) Interannual and interdecadal snowfall variability must be more seriously considered when assessing the rapid ice volume changes that are occurring over Antarctica. With regard to interannual variability, consider a recent estimate of Antarctic ice sheet mass loss that is the equivalent of 0.4 ± 0.2 mm year^{-1} GSL rise for 3 years (2002–2005) from satellite-derived time-variable gravity measurements (*28*). Antarctic-wide annual snowfall accumulation decreased by about 25 mm y^{-1} WEQ, or about 0.86 mm year^{-1} GSL rise, between calendar year 2002 and 2003 (Fig. 3), suggesting that the gravity fluctuations could be heavily influenced by interannual snowfall variations.

With regard to interdecadal variability, the ERA-40 snowfall accumulation is about 22 mm year^{-1} WEQ lower over WAIS for the past decade (1995–2004) compared with the previous decade (1985–1994) (Fig. 3), the GSL equivalent of 0.18 mm year^{-1}. This signal is of the same order as the 47 Gton (0.13 mm year^{-1} GSL equivalent) mass imbalance reported for WAIS (defined by a slightly different area) from satellite radar altimetry for roughly the past decade (*10*). In neither decade is the snowfall accumulation statistically significantly different from the 50-year WAIS mean, suggesting that such fluctuations are normal. The cause of the recent mass imbalance will remain unclear until a longer satellite record is available, but it may be partly related to accumulation variability.

2) Antarctic snowfall is not currently compensating for the oceanic-induced melting at the ice sheet periphery. If anything, our 50-year perspective suggests that Antarctic snowfall has slightly decreased over the past decade, while global mean temperatures have been warmer than at any time during the modern instrumental record (*26*). Radiosonde and ERA-40 temperature data indicate a uniform winter warming trend in the mid-troposphere over Antarctica since the early 1970s, but seasonally averaged ERA-40 precipitation data suggest that there has been no commensurate increase in winter snowfall since at least 1985 (*12*). These findings suggest that atmospheric circulation variability, rather than thermodynamic moisture increases, may dominate recent Antarctic snowfall variability.

Our technique of synthesizing observational records with model reanalysis has provided a coherent record of Antarctic-wide snowfall accumulation variability extending back before the modern satellite era. As more and improved (e.g., ground-penetrating radar) accumulation records become available, it will be possible to revisit this study with greater accuracy. A longer (1 to 2 centuries) reconstruction was not possible because of the limitations of the current data set but clearly is necessary to better understand the multidecadal Antarctic accumulation variability. Satellite-based techniques show great promise for precisely measuring Antarctic ice mass changes. It is critical to extend these records to distinguish thickening or thinning signals from snowfall variability.

Our results indicate that there is not a statistically significant global warming signal of increasing precipitation over Antarctica since the IGY, inferring that GSL rise has not been mitigated by recently increased Antarctic snowfall as expected. It may be necessary to revisit GCM assessments that show increased precipitation over Antarctica by the end of this century in conjunction with projected warming (*29*). Vigorous efforts are needed to better understand this remote but important part of the planet and its role in global climate and sea level rise.

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Divergent Induced Responses to an Invasive Predator in Marine Mussel Populations

Aaren S. Freeman* and James E. Byers

Invasive species may precipitate evolutionary change in invaded communities. In southern New England (USA) the invasive Asian shore crab, *Hemigrapsus sanguineus*, preys on mussels (*Mytlius edulis*), but the crab has not yet invaded northern New England. We show that southern New England mussels express inducible shell thickening when exposed to waterborne cues from *Hemigrapsus*, whereas naïve northern mussel populations do not respond. Yet, both populations thicken their shells in response to a long-established crab, *Carcinus maenas*. Our findings are consistent with the rapid evolution of an inducible morphological response to *Hemigrapsus* within 15 years of its introduction.

Anthropogenic introductions increasingly bring organisms into contact that have no shared evolutionary history, which results in novel interactions between non-native and native competitors, prey, and predators (*1*). These novel species combinations create potentially strong selection pressure that can drive evolutionary change of heritable traits (*1*–*3*). Although several studies have shown that invaders can evolve rapidly in a novel, invaded environment (*1*), examples of invader-driven rapid evolutionary change in native species are rarer (*1*, *3*, *4*). Rapid evolutionary change may particularly influence the ability of native prey to recognize and respond to novel invasive predators with inducible morphological defenses.

Inducible defenses are the expression of alternative forms (phenotypic plasticity) by organisms in response to cues from a predator or competitor. Some commonly noted inducible defenses include shape changes in barnacles, spines on bryozoans and cladocerans, thickened shells of mollusks, defensive chemicals in plants, and morphological and behavioral characters in anuran tadpoles (*5*, *6*). Although selection may act on inducible defenses (*5*), in terms of both the degree of plasticity (*7*) and the prey's capacity to recognize cues from predators (*8*, *9*), to date there have been no examples of an invasive species driving the rapid evolution and emergence of an inducible morphological response. To test for the evolution of predator recognition and expression of inducible morphological defenses in a marine mussel (*Mytilus edulis*), we juxtaposed the induced defenses of two mussel populations having different historical contact with two invasive crab predators.

The Asian shore crab, *Hemigrapsus sanguineus*, was first reported in North America in New Jersey in 1988 and currently ranges from North Carolina to the midcoast of Maine, U.S.A. (*10*, *11*). *M. edulis* is a large component of *H. sanguineus*' diet (*12*), but perhaps because this is a novel predator in the North Atlantic Ocean, nothing is known about inducible defenses in mussels to this crab. A longer term resident of New England, the green crab, *Carcinus maenas*, was introduced from Europe to the Mid-Atlantic United States in 1817 and currently ranges from New Jersey, U.S.A., to Prince Edward Island, Canada (*13*). *C. maenas* has had substantial impacts on native communities throughout its introduced range (*13*–*15*) and is known to induce defenses in *M. edulis* from several populations (*14*, *16*, *17*). Small mussels are vulnerable to both crab species (*12*), show high relative growth amenable to detecting induced defenses, and represent a crucial, prereproductive stage under strong selection.

Given the invasion history of these two crabs, *M. edulis* in northern New England (specifically northeastern Maine) has never experienced predation by *H. sanguineus*. Because the genus *Hemigrapsus* is not native to the Atlantic, neither have they been exposed to any *Hemigrapsus* congeners. However, they have experienced predation by *C. maenas* for more than 50 years. In contrast, mussels in southern New England have experienced predation by *C. maenas* and *H. sanguineus* for 100+ and ~15 years, respectively. To determine whether natural selection has altered the mussels' capacity to respond to these two crabs, we quantified the responses of mussels from these northern and southern populations to these two crab predators. If predator cues are species-specific, and if selection has altered the capacity of mussels to recognize and respond to these invasive predators, we expected that mussels from southern New England would respond to cues from both crabs, whereas northern mussels would respond to cues from *C. maenas* but not *H. sanguineus*.

To compare the inducible defenses of mussels from northern and southern New England in response to *C. maenas* and *H. sanguineus*, we collected mussels (13- to 20-mm shell length) from floating docks at six sites each in northern Maine and southern New England and brought them to Northeastern University's Marine Science Center at Nahant, MA (Fig. 1) (*18*). These mussels were then raised with nonlethal, waterborne cues from *C. maenas*, *H. sanguineus*, or no predator (control). Using the final measurements of each mussel's shell thickness index (STI), adjusted to its initial STI, we assessed the development of inducible defenses (*19*). After 3 months, mussels had grown, and mussels from northern and southern New England had thickened their shells differently in response to waterborne cues from the two invasive crab predators (i.e., there was a significant population by predator treatment interaction) (*20*). Mussels from southern sites thickened their shells in response to waterborne cues from *H. sanguineus* relative to controls ($P = 0.011$), and mussels appeared to thicken their shells in response to *C. maenas*, although the trend was not significant ($P = 0.145$) (Fig. 2). In contrast, although mussels from northern sites developed significantly thicker shells in response to cues from *C. maenas* ($P = 0.001$), they did not respond to cues from *H. sanguineus* ($P = 0.573$) (Fig. 2). In addition, there were clear population differences in the temperature-sensitive process of shell accretion, with mussels from northern populations thickening their shells more than mussels from southern populations (Fig. 2). These findings suggest that northern and southern mussel populations are

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