respectively, dust and sea salt aerosols; cloud liquid water and cloud ice mixing ratio; and number concentrations of cloud droplets and ice crystals. Transport, dry, and wet deposition, and chemical transformations of the aerosols and gaseous precursors are calculated online with the GCM. We used the autoconversion rate of cloud droplets to form rain drops and the accretion rates of cloud droplets by (*26*).

15. The reference simulation ECHAM-CTL and the preindustrial climate simulation ECHAM-PI are 5-year integrations after an initial adjustment of 3 months, whereas the simulations with no aerosol indirect effects, ECHAM-NO-AIE, and cloud lifetime effect (second indirect effect) only, ECHAM-2ND-AIE, were integrated for 3 years after the initial 3-month adjustment.
16. It is not possible to only include the cloud albedo effect in a present-day simulation because if CDNC is constant in the cloud microphysics, then the precipitation efficiency, the cloud lifetime, and the cloud liquid water path of water clouds change. This has a stronger implication for cloud radiative effects than expected from the cloud albedo effect alone. Furthermore, all simulations include aerosol direct effects.
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Climate Change and Latitudinal Patterns of Intertidal Thermal Stress

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The interaction of climate and the timing of low tides along the West Coast of the United States creates a complex mosaic of thermal environments, in which northern sites can be more thermally stressful than southern sites. Thus, climate change may not lead to a poleward shift in the distribution of intertidal organisms, as has been proposed, but instead will likely cause localized extinctions at a series of "hot spots." Patterns of exposure to extreme climatic conditions are temporally variable, and tidal predictions suggest that in the next 3 to 5 years "hot spots" are likely to appear at several northern sites.

A central goal in exploring the consequences of global climate change is to accurately predict the alteration of thermal stresses on organisms and the subsequent impact of stress on the distribution patterns of species. Specifically, the prediction that species distributions will shift poleward as global warming continues depends on the idea that thermal stresses are always higher at their more-equatorial ends. Because they are assumed to live very close to their thermal tolerance limits (*1–4*), organisms inhabiting the rocky intertidal zone have emerged in recent years as potential harbingers of the effects of climate change on species distributional patterns in nature (*3–9*). To explore these patterns, scientists working in coastal environments typically rely on air and water temperatures as proxies for body temperatures (*5–10*). Although this approach is appropriate for subtidal organisms (*10*), the body temperatures of intertidal organisms during aerial exposure at low tide are, in contrast, driven by multiple climatic factors, and can be very different from air or water temperatures (*11–18*). Furthermore, the mechanics of heat flux depend to a large extent on organism morphology, material properties, and color; thus, two organisms exposed to identical climatic conditions can display very different body temperatures (*11–16*). Lastly, whereas the temperatures of intertidal organisms are driven by terrestrial climatic factors, the timing of the alternating exposure to terrestrial and marine environments is driven by the dynamics of the tidal cycle. However, despite the observation that body temperatures are often much higher during aerial exposure at low tide than during immersion (*15–18*), and although (in temperate regions) thermal damage of proteins occurs at temperatures almost exclusively experienced during aerial exposure (*19–22*), most studies to date have focused only on geographic patterns of water temperature in setting the distribution of intertidal species (*5–10*, *23*). Under such a model, climate change is predicted to cause a poleward shift in species distributions as temperatures at the equatorial end surpass the physiological tolerances of the species in question (*3*, *6*, *7*).

We explore how thermal stress in rocky intertidal habitats varies along a latitudinal gradient, and we provide evidence that body temperatures do not increase monotonically with decreasing latitude. We focus on the intertidal mussel *Mytilus californianus*, an abundant and widely distributed species that is a competitive dominant in the intertidal ecosystem (*24*); however, the issues that we describe apply to all intertidal species (*16*). We deployed a series of temperature loggers modified to thermally match living mussels (*25*) in mussel beds (*26*) at eight sites spanning 14° of latitude ranging from northern Washington to Point Conception, California (*27*). Sites were not chosen at random or at fixed intervals; instead, we selected locations where previous intertidal studies have been conducted (*17*, *19–21*, *24*, *28–31*) in an effort to place these sites in a comparative framework with one another with regard to thermal stress.

Data from each instrument were summarized using two temperature metrics. The 99th percentile of all temperatures recorded from May to September at each site was calculated as the summer maximum, a measure of "acute" stress (*17*, *32*). The average daily maximum [(ADM), the average of all daily peaks] was also calculated for each month as a measure of "chronic" high-temperature exposure (*17*), and the highest monthly value of ADM for each site was considered as the peak ADM. Data were analyzed using a Kruskal-Wallis test (Statview), which was used to rank sites in descending order from "hottest" to "coolest" for comparison with the null model of monotonically increasing thermal stress with decreasing latitude (*33*).

Results clearly indicated that body temperatures did not become more thermally stressful with decreasing latitude, and that the patterns of stress varied to some extent with the temperature metric in question (Fig. 1). There was no clear latitudinal pattern in either of the temperature metrics. Whereas conditions were slightly hotter at Jalama and Alegria, California, two wave-protected sites near Point Conception (Fig. 1), Boiler Bay and Strawberry Hill, Ore-

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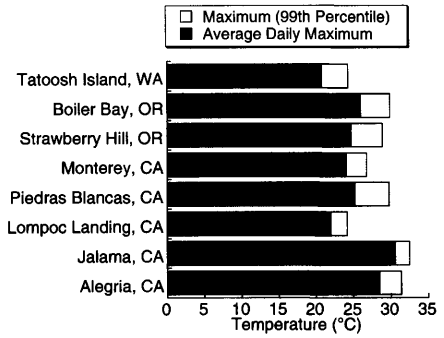

Fig. 1. "Acute" (99th percentile of temperatures) and "chronic" high-temperature (peak ADM) exposures calculated at each site in 2001, collected using temperature loggers designed to mimic the thermal characteristics of real mussels along the West Coast of the United States. Sites are arranged in order of increasing latitude (Tatoosh at the northern end). Results of a Kruskal-Wallis test indicated that levels of high-temperature stress do not change monotonically with latitude: Acute temperature stress, $H = 14.4$, $P \leq 0.05$, Alegria > Jalama > Boiler Bay > Piedras Blancas > Strawberry Hill > Monterey Bay > Tatoosh > Lompoc; Peak Average Daily Maximum, $H = 17.8$, $P \leq 0.01$, Alegria > Jalama > Boiler Bay > Piedras Blancas > Strawberry Hill > Monterey Bay > Lompoc > Tatoosh. An analysis of site means using linear regression confirmed that there is no trend in either temperature metric with latitude (Acute stress: $P = 0.40$, $r^2 = 0.12$; ADM: $P = 0.21$, $r^2 = 0.25$).

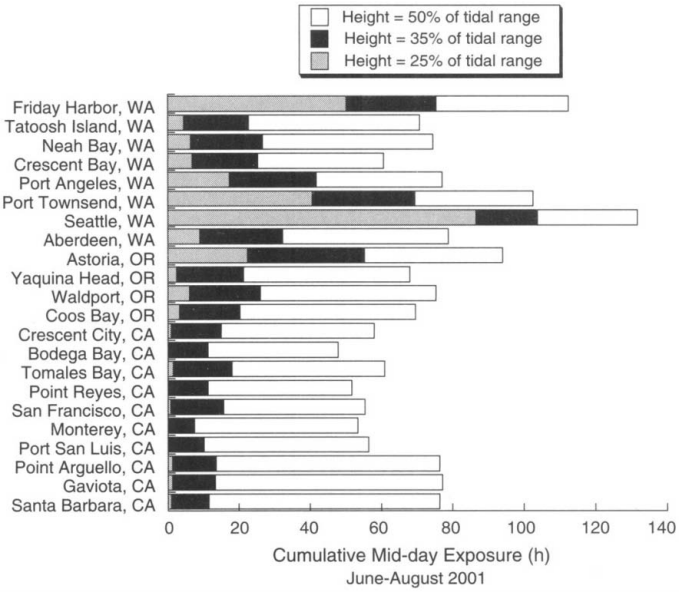

Fig. 2. Cumulative hours of midday (11:00 to 13:00) exposure for June to August 2001, based on predictions of still tidal height. Tide heights at each location were scaled to the overall summer range for 2001. The three tidal heights shown here roughly correspond to the tidal heights of mussel beds. Variability among sites is most pronounced at low intertidal heights.

gon (two of the most northerly sites considered), were also among the hottest sites measured. Lompoc Landing, California, one of the more southern sites, was thermally very similar to Tatoosh Island, Washington, the northernmost site where instruments were deployed. Data also indicated that the timing of maximum stress varied between sites. Acute temperature exposures occurred from May to June at sites south of Monterey, California, and from June to July at sites north of Monterey.

Patterns in thermal stress based on body temperatures experienced during aerial exposure thus generate patterns that differ from the monotonic decrease predicted from measurements of sea surface temperature (*6*), and such patterns have potentially important consequences for how we view range boundaries and the effects of climate change on intertidal communities. Our results are consistent, for example, with data reported by Sagarin and Gaines (*34*, *35*), who have shown that many intertidal species, including *M. californianus*, do not exhibit an "abundant center" distribution. Instead, they display a complex pattern whereby peaks in abundance are shifted toward one end of each species' range, or else show no clear pattern at all. Our results are also supported by recent data from Gilman (*36*), who found no relation between latitude and temperature stress in a study of the northernmost limit of an intertidal gastropod.

Although variability in local climate and wave splash undoubtedly plays an important role in driving geographic patterns of thermal stress during aerial exposure, perhaps the single largest factor affecting these patterns is variability in the timing of low tides. During summer months at many northern sites in the Northeast Pacific, extreme low tides ("spring" tides) often occur midday, when climatic conditions are hottest. In contrast, many summertime extreme lows at more southern sites occur in the middle of the night, and animals remain submerged during the hottest parts of the day. As a result, even if terrestrial climatic conditions become progressively hotter as one moves south along the West Coast, as they likely do, animals at southern sites may be afforded considerable protection by being submerged during the hottest parts of the day. Such interactions between tidal cycle and terrestrial climate have been noted (*18*, *37*, *38*), but these patterns have never been explicitly tested.

To estimate how the patterns we observed might be related to variability in tidal patterns, still tidal height estimates were calculated at 20 stations ranging from Friday Harbor, Washington (48.55°N, 123.00°W), to Santa Barbara, California (34.42°N, 119.68°W) (*39*). Previous measurements and models of mussel body temperatures (*15*–*18*) have indicated that maximum high-temperature stress in this species occurs during midday (11:00 to 13:00), the period of maximum solar insolation. As a result, all other factors being equal, we consider midday exposures during summer months to be the "riskiest" in terms of exposure to extreme climatic conditions. As a measure of the role of the tide in exposing organisms to potentially damaging thermal conditions, we calculated the total duration of midday exposure for the months of June, July, and August at each site for a period of 25 years (1985–2009). Estimates were calculated at 25-cm intervals of still tidal height, from Mean Lower Low Water (MLLW) −1 m to MLLW + 2.25 m, and were then normalized to the tidal range of each site. Although spatial and temporal patterns change with tidal height, here we focus on midtidal heights most relevant to mussel distribution.

As predicted from our temperature data, during the climatically hottest times of year in 2001 organisms at mid- to low tidal heights (heights relevant to mussel beds) at most southern sites experienced little or no midday exposure (Fig. 2). Differences between sites were most pronounced at lower tidal heights, suggesting that the patterns we observed are particularly relevant to mid- and low intertidal species.

Analysis further indicated that the duration of midday exposure can vary markedly over time and that the magnitude of this temporal variability changes from site to site (Fig. 3). As described by Denny and Paine (*40*), tides display an 18.6-year cycle due to an oscillation in the declination of the moon's orbit relative to the plane of Earth's equator. Denny and Paine showed that at one site (Tatoosh Island) this variability was sufficient to cause observable shifts in the zonation height of mussels (*40*). Our analysis of the total summertime exposure to midday environmental conditions shows that not only does year-to-year variability differ in amplitude from site to site but also that peaks in midday exposure are slightly out of phase with one another at the different sites (Fig. 3). For example, at Friday Harbor, the total summertime midday exposure at a midtidal height varies only slightly from year to year, ranging from a low of 102 hours in 1994 to a maximum cumulative exposure of 120.5 hours in 2003 (Fig. 3). In contrast, sites at Monterey show a much greater variation from year to year, with a low of 30 hours in 2008 to a high of 64 hours in

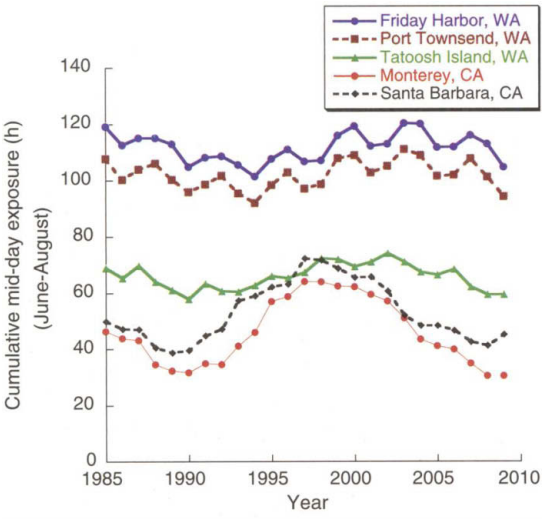

Fig. 3. Change in midday exposure during summer (June to August) at select sites along the West Coast. Data are shown for the mid (50%)-range tidal height (scaled to the average tidal range for the period 1985–2004) at each site. Southern sites (Monterey and Santa Barbara, California) showed a high interannual range, with peaks in exposure occurring in the mid to late 1990s. In contrast, peak midday exposures at northern sites are not predicted to occur until 2003.

1997 (Fig. 3). In general, sites in central and southern California showed peaks in midday exposure during the years 1997–98, and those in central Oregon were at a maximum in 1999. In contrast, examination of tidal heights predicts that maximum exposure at many northern Washington sites will occur in 2003 (Fig. 3). Indeed, large mussel mortality events occurred in the summer of 2002 in both Washington (*41*) and Oregon (*42*). These results suggest that, all other factors being equal, the relative level of thermal stress observed between these sites will vary markedly over time. If the mussel temperature measurements described here had been conducted in 1997, we may indeed have observed an increase in thermal stress with decreasing latitude (although given the disparity in exposure times, this is not a foregone conclusion). However, these projections indicate that in the next 3 to 5 years, though summer midday exposure will be near maximum at many northern sites, exposure will approaching a minimum at many southern sites (Fig. 3). As a result, we are entering a period lasting the next few years where a change in temperature [whether through El Niño–Southern Oscillation (ENSO), climate change, or stochastic processes] is most likely to impact intertidal organisms at northern "hotspots" and not necessarily at more southern sites.

Thermal stress during aerial exposure is not the only factor determining the distribution of intertidal species along the West Coast. Larval dispersal is likely to play an important role (*10*), as are food supply (*31*) and biotic interactions such as predation and competition (*4*, *24*, *43*). Water temperature also has been shown to have strong physiological impacts on intertidal invertebrates. Sanford (*44*), for example, showed that water temperature appears to drive the rate of feeding and assimilation by seastars. However, our results demonstrate that predictions of the effects of climate change based on body temperatures generate predictions that differ markedly from those based only on air or water temperature. We further show that because of the coupled effects of the timing of aerial exposure with terrestrial climate, latitudinal patterns of thermal stress are not only highly complex in space but also in time. Without a mechanistic, quantitative understanding of what the temperatures of ectothermic organisms are in nature, our ability to forecast the effects of anticipated changes in climate on organismal physiology and biogeography will be severely limited.

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26. Instruments were deployed in approximate growth position (posterior end upward) in mussel beds in the midintertidal zone at each site. To eliminate the effects of substratum angle on temperature (*2*, *17*, *30*), loggers were attached with epoxy to horizontal, unshaded rock surfaces. Each instrument was programmed to record average temperatures at 10- to 15-min intervals at a resolution of 0.3°C and recorded continuously throughout the entire year of 2001. Between 3 and 10 loggers were deployed at each site, but instrument losses due to wave action were high so 2 to 6 loggers were recovered from each site.
27. Sites included (in decreasing order of latitude): Tatoosh Island, Washington (48.39°N, 124.74°W); Boiler Bay, Oregon (44.83°N, 124.05°W); Strawberry Hill, Oregon (44.25°N, 124.12°W); Monterey Bay, California (Mussel Point; 36.63°N, 121.90°W); Piedras Blancas, California (35.66°N, 121.29°W); Lompoc Landing, California (34.72°N, 120.61°W); Jalama, California (34.50N, 120.50°W); and Alegria, California (34.47°N, 120.28°W). Instruments were deployed at five additional sites, but temperature records did not span the entire summer and so these sites are not included here.
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