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Phanerozoic Earth System Evolution and Marine Biodiversity

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The Phanerozoic fossil record of marine animal diversity covaries with the amount of marine sedimentary rock. The extent to which this covariation reflects a geologically controlled sampling bias remains unknown. We show that Phanerozoic records of seawater chemistry and continental flooding contain information on the diversity of marine animals that is independent of sedimentary rock quantity and sampling. Interrelationships among variables suggest long-term interactions among continental flooding, sulfur and carbon cycling, and macroevolution. Thus, mutual responses to interacting Earth systems, not sampling biases, explain much of the observed covariation between Phanerozoic patterns of sedimentation and fossil biodiversity. Linkages between biodiversity and environmental records likely reflect complex biotic responses to changing ocean redox conditions and long-term sea-level fluctuations driven by plate tectonics.

Identifying the causes of changes in biodiversity and mass extinctions in Earth history is a central goal of paleobiology (1, 2). However, patterns of taxonomic richness and turnover derived from paleontological data covary with changes in the sedimentary rock record, thereby raising the possibility that the fossil record is strongly overprinted by geologically controlled sampling biases (3–6). An alternative hypothesis is that large-scale geological processes cause physical environmental changes that influence both patterns of sedimentation and macroevolution (3, 7). The sampling bias and common-cause hypotheses are not mutually exclusive, and a critical unanswered question is their overall relative importance during Earth's history.

To address this question, we used a recent compilation of geographically and temporally explicit co-occurrences of Phanerozoic rocks and fossils in North America (7). We compared fossil diversity and sedimentary rock quantity according to the common analytical currency provided by macrostratigraphy: The total number of fossil taxa in

a time interval is commensurable with the total number of hiatus-bound rock packages, which relate to the underlying geological processes that control the spatial and temporal distribution of sedimentation (8). To evaluate the possible role of common-cause interactions in driving both the macroevolutionary history of marine animals and continent-scale patterns of sedimentation, we compared the rock and fossil records to a global database of isotope ratios in marine carbonates (9) and to estimates of relative global sea level (10, 11), all of which have been linked to biological turnover. We restricted our analysis to the marine component of the stratigraphic and fossil data (Fig. 1A), which dominates the North American record (7, 12).

In the Phanerozoic, fluctuations (but not the trend) in low-latitude carbonate $\delta^{18}\text{O}$ (Fig. 1B) reflect global climate change, which has been linked to biodiversity patterns (13) and some mass extinctions (14). Changes in $\delta^{13}\text{C}$ (Fig. 1C) are controlled by the exchange of carbon between isotopically depleted organic and isotopically enriched inorganic reservoirs (15, 16), and $\delta^{13}\text{C}$ excursions commonly coincide with turnover events in the fossil record (17). The burial efficiency of pyrite formed through microbial sulfate reduction plays a key role in the Phanerozoic $\delta^{34}\text{S}$ pattern (Fig. 1D) (18, 19). Seawater $^{87}\text{Sr}/^{86}\text{Sr}$ (Fig. 1E) is

governed by the flux and composition of Sr from midocean ridge volcanism and from continental weathering (20). Both $^{87}\text{Sr}/^{86}\text{Sr}$ and $\delta^{34}\text{S}$ covary with generic origination rate over the Phanerozoic (21). Finally, global long-term sea level, expressed geologically as the extent of continental flooding (Fig. 1F), has been recognized as a potential control on marine diversity via a species-area effect (3, 22).

Interval-to-interval changes (i.e., first differences) in the number of marine animal genera (G; representing face-value range-through diversity) were positively correlated with first differences in the total number of marine sedimentary rock packages (P). We found the highest Spearman rank-order correlations between the G and P records, between P and sea level, and between $\delta^{34}\text{S}$ and $^{87}\text{Sr}/^{86}\text{Sr}$ (table S1). Multiple linear regression of the six detrended environmental variables on G (adjusted $R^2 = 0.28$; $P = 0.00004$) similarly showed P as the dominant explanatory variable ($P = 0.00004$), with the next strongest contribution from $\delta^{34}\text{S}$ ($P = 0.09$). Simple correlation and regression analyses of detrended data seemed to support aspects of the rock-record bias hypothesis. However, first differences emphasize only the shortest-term variability in the data, which is expected to be strongly overprinted by variability in sampling. Moreover, simple correlation and regression analyses are only sensitive to linear or monotonic relationships among variables.

To overcome these limitations, we used a non-parametric measure of information transfer (IT) to assess the relative strength and directionality of interactions among G, P, and several global environmental records (23). Unlike correlation, the IT between two variables, A and B, is nonsymmetric ($A \rightarrow B \neq B \rightarrow A$) and can be used to distinguish a driving variable from a response variable, even in short and unevenly sampled time series (fig. S1) (24). We first quantified the relative strength of IT from each potential driving factor on a response variable, while excluding any IT that may arise from common interaction with other factors (e.g., does sea level contain significant information on generic richness beyond any mutual correlations with the sedimentary rock

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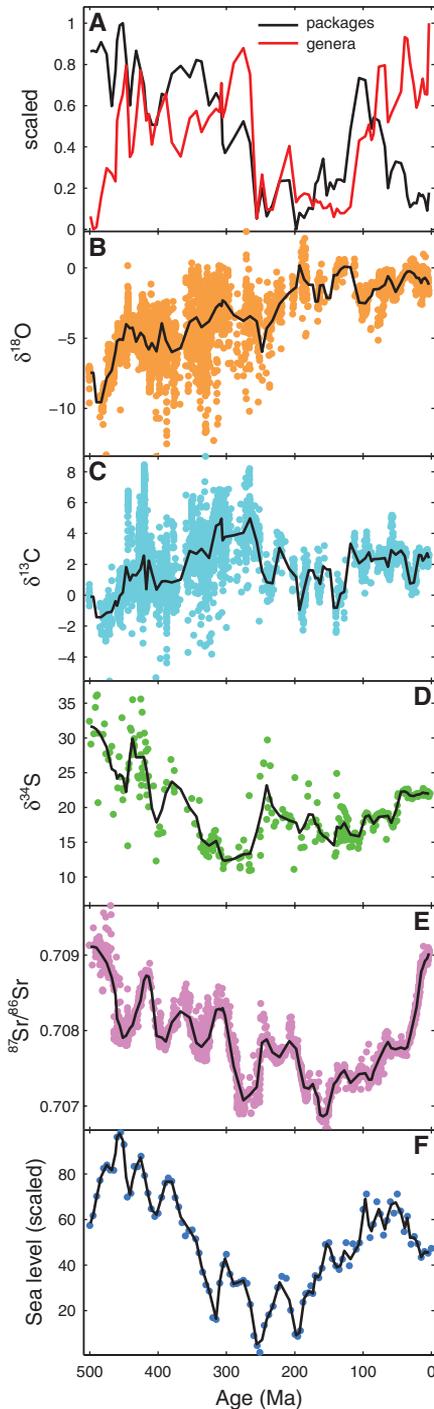


Fig. 1. Environmental variables related to Phanerozoic Earth system evolution (Ma, millions of years ago). **(A)** Total number of marine genera (red), based on North American fossil occurrences, and total number of marine sedimentary packages [black (7)] in North America. **(B to E)** Isotope ratios from marine carbonates (9). $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ records are the low-latitude subsets. Solid black lines are averages for the time bins in (A), which are used for time series analyses. **(F)** Global estimates of continental flooding (blue) in 5-million-year bin averages (21) resampled (black) at the bin midpoints of 80 time intervals (median duration, 5.3 million years) from the Late Cambrian through the Pliocene.

record?). Significance levels were established by iteratively randomizing the driving variable (fig. S2). We refer to this analysis as conditional IT (CIT) and interpret the results in terms of relative strength of statistical dependence and information redundancy. We next tested whether the IT between two variables is significantly directional when compared to a large number of surrogate time series. Surrogates are replicates of the original data that preserve amplitudes and frequencies but randomize frequency domain phases, thereby operationally distinguishing between correlation and causation (fig. S1). We refer to this analysis as directional IT (DIT) and interpret the results in terms of asymmetric information flow resulting from underlying driver-response relationship (24). If two indirect proxy records are equally sensitive to a common forcing mechanism, then DIT between the two variables is comparable in both directions and both will be redundant in CIT analyses against a third variable. However, if one variable is more sensitive to a common mechanism, then it will be a better predictor of the other. IT can also detect nonlinear relationships (figs. S1 and S2) and does not filter out low-frequency patterns (fig. S3).

Using this approach, we found that several of the Phanerozoic global environmental records provide significant IT on North American marine generic diversity, even after conditioning for the total number of rock packages (Fig. 2). Of those proxies, the $\delta^{34}\text{S}$ and sea-level records exhibited the strongest CIT on marine diversity (Fig. 2, A and B). Conversely, the IT from sedimentary rock packages, $\delta^{18}\text{O}$, $\delta^{13}\text{C}$, and $^{87}\text{Sr}/^{86}\text{Sr}$ to diversity is relatively weak or not significant when conditioned on $\delta^{34}\text{S}$ and/or sea level (Fig. 2, D to F). DIT analyses of diversity against sea level and $\delta^{34}\text{S}$ show that these relationships are significantly directional, with information flowing from the environmental variables to diversity (Fig. 2, G and H). We also find near-significant directional IT from G to P (Fig. 2I). Although this result may seem counterintuitive, if common-cause mechanisms are affecting both G and P, and if G is generally more sensitive than P to these changes (Fig. 2, A and B), then information will appear to flow from G to P in DIT analyses.

The paleoenvironmental records used here capture a mixture of signals from global climate, tectonics, and biogeochemical cycling that are

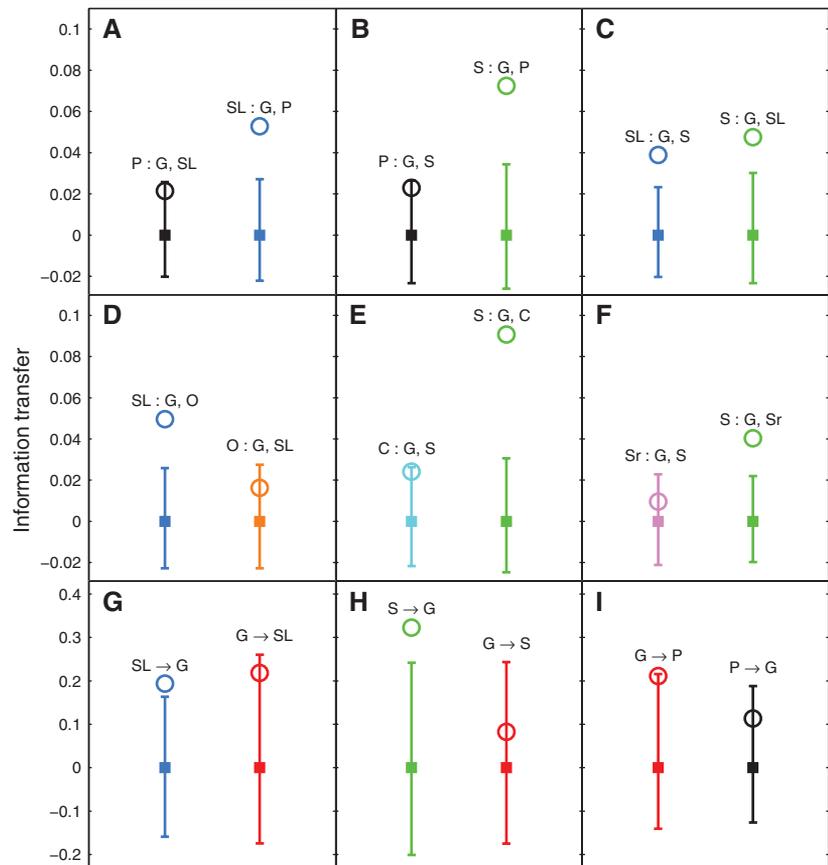


Fig. 2. Information transfer (IT) relationships between Phanerozoic environmental records and marine diversity. **(A to F)** Conditional IT from X to Y given Z ($X:Y, Z$) (open circles). Values are integrated IT (area under IT curve) (23). Solid squares and error bars represent null distributions encompassing 95% of 1000 IT calculations using randomized X or Z . **(G to I)** Directional IT from X to Y ($X \rightarrow Y$) and vice versa. Error bars encompass 95% of 5000 IT calculations using amplitude-adjusted Fourier transform surrogates. All IT distributions are zero-mean centered. Colors correspond to the variables in Fig. 1. P, total number of packages; G, total number of genera; SL, sea level; S, $\delta^{34}\text{S}$; O, $\delta^{18}\text{O}$; C, $\delta^{13}\text{C}$; Sr, $^{87}\text{Sr}/^{86}\text{Sr}$.

intertwined and that may reflect common-cause mechanisms. Thus, interpreting these IT results minimally requires that the interdependence among the environmental variables be considered. IT analysis (fig. S4) detects significant statistical dependence between the $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ records, between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, and between $\delta^{34}\text{S}$ and $^{87}\text{Sr}/^{86}\text{Sr}$. DIT indicates a dominant flow of information from $\delta^{13}\text{C}$ to $\delta^{34}\text{S}$ (fig. S4G), which is consistent with the expectation of a redox-controlled coupling of the global carbon and sulfur cycles (15, 16), possibly involving the long-term impact of organic carbon on pyrite burial efficiency and its effect on the sulfur isotopic chemistry of the ocean (25). DIT from $\delta^{13}\text{C}$ to $\delta^{18}\text{O}$ is also significant (fig. S4H), suggesting that carbon cycling is indeed a driver of climate changes on this time scale (9). Intriguingly, IT is directional from $\delta^{34}\text{S}$ to $^{87}\text{Sr}/^{86}\text{Sr}$ (fig. S4I), which makes the $^{87}\text{Sr}/^{86}\text{Sr}$ record redundant with $\delta^{34}\text{S}$ in conditional analyses (Fig. 2F) and suggests that the latter is more sensitive to common forcing mechanisms, such as

changes in mid-ocean ridge length and rates of hydrothermal alteration of sea floor basalt. Sea level is the dominant environmental signal in P (fig. S4, D to F), supporting previous claims that changes in the number of marine rock packages reflect expansions and contractions of epicontinental seas.

The lack of redundancy between sea level and $\delta^{34}\text{S}$ with respect to diversity in CIT analyses (Fig. 2C) suggests that $\delta^{34}\text{S}$ captures biologically important information about oceanographic conditions, such as average shelf redox conditions, that is not reflected in sea-level estimates alone. IT analysis does, however, show that $\delta^{34}\text{S}$ is linked to both sea level and $\delta^{13}\text{C}$ (fig. S4A). This coupling may reflect the positive effect that expansions in shallow epicontinental seas can have on the burial of organic carbon and associated pyrite (26) and the effect that sea level decrease can have on the exposure and weathering of carbon- and pyrite-rich marine sediments.

The analyses above use face-value data from the fossil record of marine animals to estimate

range-through diversity in North America. The fact that there is significant IT flowing from environmental variables to the diversity data provides prima facie evidence for the hypothesis that there is a biological signal in the face-value fossil record. If North American genus ranges are based on their global occurrences (Fig. 3A), which should provide better estimates of their true times of global extinction and origination, then we obtain even stronger IT relationships with the same global environmental variables (fig. S5). Nonetheless, diversity estimates are strongly affected by variation in sampling intensity (I). To address this, we compared face-value diversity estimates to the corresponding number of fossil collections (Fig. 3B) and to sampling-standardized diversity estimates for North American marine animal genera (Fig. 3C) (27).

First differences in the number of fossil collections were strongly positively correlated with first differences in diversity (table S1). IT analysis confirmed that face-value diversity contains a significant and strong signal from the number of collections (Fig. 3D), but IT also indicated that face-value diversity is a better predictor of sampling-standardized diversity than vice versa (Fig. 3E). This result can be intuited by examining the striking similarities between the raw and standardized diversity curves (fig. S6). The number of collections also exhibited a significant IT relationship with sea level but not with $\delta^{34}\text{S}$ (Fig. 3, F and G, and fig. S7), whereas the opposite was true for sampling-standardized diversity (Fig. 3, H and I, and fig. S8). IT from sea level to face-value diversity was significant beyond shared information with collections (fig. S9). Together, these results suggest that the relationship among $\delta^{34}\text{S}$, sea level, and face-value diversity is sufficiently robust to transcend sampling variability. These results also suggest that the number of fossil collections may carry a significant environmental signal related to changes in sea level (Fig. 3F) that may be removed by some sampling-standardization techniques.

Over the Phanerozoic as a whole, our results indicate that there is a geological coupling between marine biodiversity in North America and global environmental changes, particularly those that affect sulfur cycling and the extent of continental flooding. An example of one such long-period geological linkage is the closing and opening of ocean basins associated with the assembly and breakup of the supercontinent Pangaea. This “Wilson cycle” of continental coalescence and dispersion is a dominant, low-frequency mode of variation in both the rock and fossil records that clearly separates the Paleozoic and post-Paleozoic into physically and biologically distinct time intervals (3, 12). This large-scale tectonic signal is also evident in the flooding history of the continents, in $^{87}\text{Sr}/^{86}\text{Sr}$ (Fig. 1), in model and proxy reconstructions of atmospheric $p\text{CO}_2$ (28, 29), and in the bimodal character of sulfur isotopic fractionation and pyrite burial flux over the Phanerozoic (30).

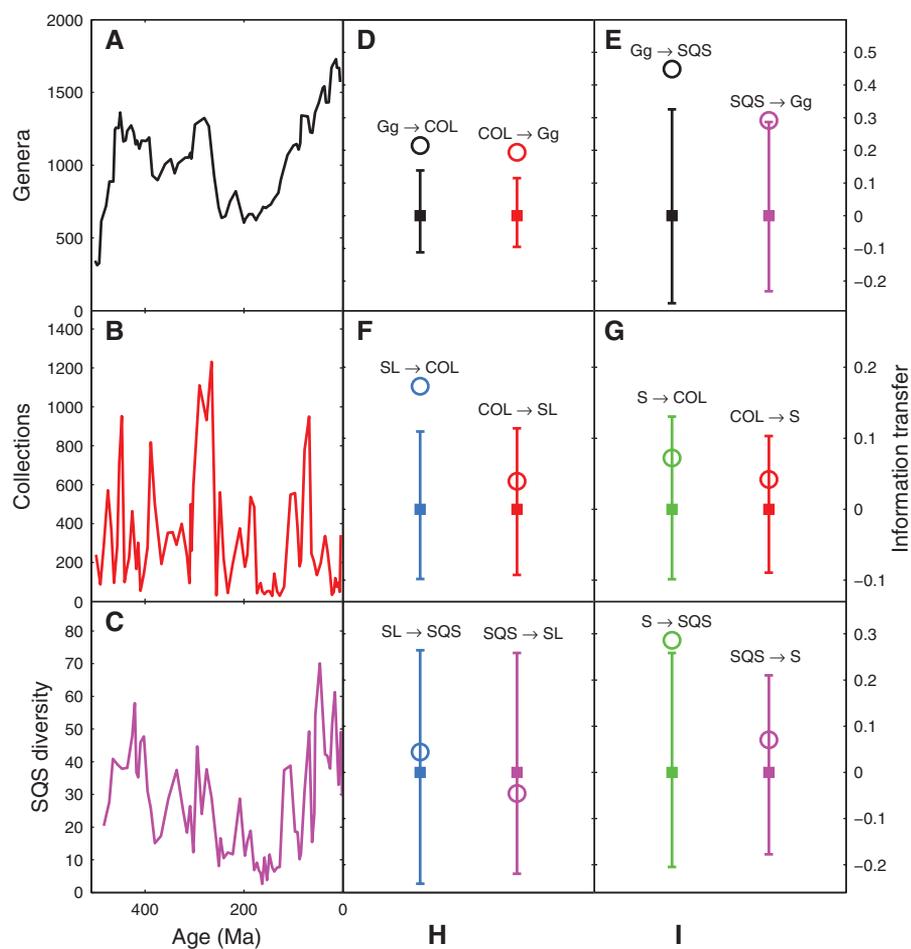


Fig. 3. IT relationships among raw diversity, collection counts, and sampling-standardized diversity. (A) Face-value marine diversity for North American genera based on global occurrences. (B) The corresponding number of fossil collections. (C) Sampling-standardized diversity estimate using shareholder quorum subsampling (SQS) (27). (D and E) Directional IT analysis shows that raw diversity contains both the collections signal and the SQS diversity signal. (F and G) Collections contains a sea-level signal but not a $\delta^{34}\text{S}$ signal. (H and I) SQS diversity contains a $\delta^{34}\text{S}$ signal but not a sea-level signal. Gg, total number of genera (global occurrences); SL, sea level; S, $\delta^{34}\text{S}$; COL, collections.

Studies targeting higher-frequency periodic signals have found statistically similar oscillations in the Phanerozoic rock and fossil records (12, 31) that are comparable to cyclic variations in $\delta^{34}\text{S}$ and $^{87}\text{Sr}/^{86}\text{Sr}$ (9). Although the presence of statistically similar frequency components suggests the presence of an underlying oscillatory mechanism, documenting such similarities in the rock and fossil records does not provide a conclusive test of the rock-record bias or common-cause hypotheses. By quantifying the relative merit of the two hypotheses in light of environmental records that are related to Phanerozoic-scale Earth system evolution, we found compelling evidence to suggest that linkages among shelf redox conditions, biogeochemical cycling, and continental flooding have played a more fundamental role in determining the Phanerozoic history of marine biodiversity (as preserved in the fossil record) than sampling biases and variability in the amount of preserved sedimentary rock. Although our results do not address the specific environmental mechanisms that were important in determining the selectivity and magnitude of individual biological turnover events, they do provide quantitative support for the hypothesis that there has been a long-term coupling between

physical environmental changes and marine biodiversity during the Phanerozoic.

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Supporting Online Material

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Materials and Methods

Figs. S1 to S9

Tables S1 and S2

References (32–41)

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Climate Change, Keystone Predation, and Biodiversity Loss

Christopher D. G. Harley

Climate change can affect organisms both directly via physiological stress and indirectly via changing relationships among species. However, we do not fully understand how changing interspecific relationships contribute to community- and ecosystem-level responses to environmental forcing. I used experiments and spatial and temporal comparisons to demonstrate that warming substantially reduces predator-free space on rocky shores. The vertical extent of mussel beds decreased by 51% in 52 years, and reproductive populations of mussels disappeared at several sites. Prey species were able to occupy a hot, extralimital site if predation pressure was experimentally reduced, and local species richness more than doubled as a result. These results suggest that anthropogenic climate change can alter interspecific interactions and produce unexpected changes in species distributions, community structure, and diversity.

Predictions concerning biological responses to climate change are largely based on the environmental tolerances of individual species and the assumption that these species will remain within their bioclimatic envelope as conditions change (1). At coarse scales, these predictions generally match observed changes in distribution and abundance across gradients such as latitude, elevation, and depth (2, 3). However, changing climatic conditions also lead to altered community composition (4) and shifts in the strength and sign of interspecific interactions

(5, 6)—changes that may greatly affect community dynamics and ecosystem function (7). Because species interactions can accelerate, retard, prevent, or even reverse predicted biotic changes based solely on simplistic models, interspecific relationships must be incorporated into the predictive framework of climate change (1, 8). Although distributional shifts forced by interspecific relationships have been demonstrated in the lab (9) and predicted by data-driven models (10), appropriate field tests are largely absent.

Rocky intertidal communities are ideal testbeds for studying the effects of climatic warming because many intertidal organisms already live very close to their thermal tolerance limits (11). Intertidal species' distributional limits are correlated with their upper thermal tolerance (12), and

changes in their distribution and abundance over time are associated with warming temperatures (13–15). However, species distributions are also strongly influenced by interspecific interactions (16), and these interactions are temperature-sensitive (6). Observed ecological patterns will therefore depend on both environmental stress and interspecific interactions (10, 17, 18).

In this study, I examined the roles of temperature and predation on the intertidal community in the Salish Sea, which spans a regional-scale thermal gradient from west to east (Fig. 1 and table S1). The oceanic terminus of the Salish Sea (the western end of the Strait of Juan de Fuca) is exposed to cool maritime weather, frequent fog and cloud cover, and early morning low tides, resulting in minimal intertidal thermal stress. The more eastern portions of the Salish Sea are warmer and sunnier, receive less cooling wave swash and spray, and feature summer low tides near midday. As a result, mid-intertidal rocks and organismal body temperatures become progressively hotter from west to east (Fig. 1) (19, 20).

To determine the ecological consequences of this spatial gradient in thermal stress, I first surveyed vertical zonation patterns of sessile invertebrate species and their principle predator. The upper limits of the mussels *Mytilus californianus* and *M. trossulus* and the barnacles *Semibalanus cariosus* and *Balanus glandula* were all negatively correlated with mid-intertidal rock temperatures (Fig. 2, A to D). In contrast, the upper foraging limit of the predatory sea star *Pisaster ochraceus* was independent of the thermal stress gradient (Fig. 2E). The slope of upper limits ver-

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