

SCIENTIFIC DATA

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SUBJECT CATEGORIES

- » Ecophysiology
- » Marine biology
- » Climate-change impacts

Data Descriptor: Long-term, high frequency *in situ* measurements of intertidal mussel bed temperatures using biomimetic sensors

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Received: 29 June 2016

Accepted: 30 August 2016

Published: 11 October 2016

At a proximal level, the physiological impacts of global climate change on ectothermic organisms are manifest as changes in body temperatures. Especially for plants and animals exposed to direct solar radiation, body temperatures can be substantially different from air temperatures. We deployed biomimetic sensors that approximate the thermal characteristics of intertidal mussels at 71 sites worldwide, from 1998-present. Loggers recorded temperatures at 10–30 min intervals nearly continuously at multiple intertidal elevations. Comparisons against direct measurements of mussel tissue temperature indicated errors of ~2.0–2.5 °C, during daily fluctuations that often exceeded 15°–20 °C. Geographic patterns in thermal stress based on biomimetic logger measurements were generally far more complex than anticipated based only on ‘habitat-level’ measurements of air or sea surface temperature. This unique data set provides an opportunity to link physiological measurements with spatially- and temporally-explicit field observations of body temperature.

Design Type(s)	observation design • time series design
Measurement Type(s)	temperature of environmental material
Technology Type(s)	biomimetic sensor
Factor Type(s)	geographic location
Sample Characteristic(s)	intertidal zone • New South Wales • Queensland • State of Victoria • Province of British Columbia • Coquimbo • England • Scotland • County Clare • Galway • County Mayo • Baja California Peninsula • Auckland Region • Canterbury Region • Coromandel Peninsula • Northland Region • West Coast Region • State of California • Commonwealth of Massachusetts • State of Oregon • State of South Carolina • State of Washington • Eastern Cape Province • KwaZulu-Natal Province • Northern Cape Province • Western Cape Province

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Background & Summary

Increasingly, researchers are emphasizing the need to consider physiological mechanisms when forecasting the effects of global climate change on organisms and ecosystems^{1–3}. Specifically, studies have highlighted a need to understand how environmental conditions vary in space and time⁴ in addition to the details of how organisms respond to those variables^{5–8} as a means of evaluating inter- and intraspecific vulnerability (‘winners and losers’)^{9,10}, the probability of invasion by non-native species^{11,12}, changes in patterns of abundance and distribution^{13,14}, and declines in biodiversity¹⁵ and ecosystem services¹⁶.

Notably, there is concern that simple correlations between environmental measurements (such as air, land surface and sea surface temperature) and species distributions may fail under the novel conditions presented by climate change¹⁷, highlighting the need to extrapolate from experiments conducted under controlled conditions to projections of future climate impacts^{3,18}. There has also been an emphasis on considering the cumulative impacts of physiological stress^{14,19} on patterns of growth²⁰ and reproduction²¹ rather than focusing solely on lethal extremes¹⁹.

However, making connections between the lab and field can be far more complex than is often assumed⁴. For example, a number of theoretical and empirical studies have explored the often over-riding importance of spatial and temporal variability in environmental parameters^{9,22}, which is not captured when experiments are based only on monthly, yearly or decadal averages^{23,24}. Moreover, while large-scale measurements of environmental conditions made by satellites, buoys, and weather stations provide critical insights into rates of environmental change on large scales²⁵, at a proximal level these habitat-level measurements may not always serve as good indicators of physiological stress^{4,26}. In fact, the only ‘environmental signals’ that matter to an organism are those that the organism actually experiences²⁷. Making connections across scales that span from organismal to biogeographic is no easy matter, but is crucial if we are to effectively forecast ongoing responses to environmental change^{28,29}.

One of the most obvious examples of the complex ways climate defines weather patterns, and weather then drives niche-level organismal responses³⁰, is how climate change is ultimately reflected as changes in plant and animal body temperatures. The vast majority of organisms on Earth are ectothermic poikilotherms, so that their body temperatures and thus levels of physiological performance change with ambient environmental conditions. For terrestrial and intertidal ectotherms (and even some shallow-water corals³¹), body temperatures are driven by multiple environmental parameters, most notably solar radiation, air and water temperatures and wind speed^{32–34}. The structure of an organism’s microhabitat, and especially its exposure to direct solar radiation, can have enormous implications for its body temperature, such that animal temperatures are only close to air temperature in fully shaded microhabitats^{26,35}. While many animals can behaviourally select among these microhabitats as a means of thermoregulation³⁶, others are functionally sessile and thus have body temperatures determined by very local topography. To further complicate matters, the size, morphology and colour of organisms, as well as their ability to form aggregations^{37,38} can affect heat exchange so that two organisms exposed to identical microclimatic conditions can have very different body temperatures^{39,40}. To contend with these issues, multiple authors have developed heat budget models that factor-in the characteristics of the organism^{26,33,41} to predict body temperatures using weather data as inputs.

An alternative approach—and one that is required to validate biophysical (heat budget) models—is to use *in situ* sensors specifically tailored to record temperatures relevant to the organism being studied, either directly or through the use of biomimics⁴². Biomimetic sensors (biomimics) match the thermal characteristics (size, morphology, colour, material properties) of living organisms^{43,44}, serving as an effective tool for recording organismal body temperature in their natural environment^{45,46}. Here we report on a long-term data set of temperatures recorded by biomimetic loggers thermally matched to bivalves (mussels) in the intertidal zone, one of the most physiologically harsh habitats on Earth. Over the course of a 24-hr period, intertidal animals and algae are alternately exposed to water at high tide and to air, wind and solar radiation at low tide. Thus, their temperature not only depends on local weather conditions but also on the timing and duration of low tide⁴⁷. We have previously shown, for example, that consistent differences in the timing of low tide relative to high levels of solar radiation create geographic mosaics in low tide temperature, where mussel body temperatures at higher latitude sites can be much higher than those at low latitude sites^{40,47,48}. As ecosystem engineers⁴⁹ mussels in particular have a large influence on the stability and biodiversity of the intertidal community and so quantifying their survival and physiological performance has significant ecosystem-level consequences^{50,51}.

Methods

We used biomimetic loggers to estimate temperatures of the mussels *Mytilus californianus* (West coast of North America), *M. edulis* and *Geukensia demissa* (East coast of North America), *M. chilensis* (Chile), *Perna perna* (South Africa) and *P. canaliculus* (New Zealand). We also deployed unmodified commercial loggers directly on rock surfaces at multiple sites (Australia, Ireland, Mexico, Scotland, U.K., U.S.) that recorded temperatures relevant to barnacles, newly settled mussels and other organisms that are sufficiently small that their temperatures mirror those of the underlying rock⁵².

Each biomimetic sensor (‘Robomussel’; Fig. 1) consisted of either a commercially-available TidbiT logger (TB132-20+50 and UTB1-001; Onset Computer Corporation, Pocasset, MA) encased in black-coloured polyester resin (Evercoat Premium Marine Resin, Illinois Tool Works, Inc.), or a real mussel



Figure 1. Epoxy ‘robomussel’ biomimetic logger (~8 cm in length) deployed in growth position in a *Mytilus californianus* bed. Loggers were designed to match the thermal characteristics of bivalves and were typically made of epoxy (as shown) but real shells filled with silicone were also used, especially for smaller (4 cm) mussels.

shell filled with silicone and encasing a Tidbit or a Thermochron iButton logger (DS1922L-F5; Maxim Integrated, San Jose, California). Both instruments are factory calibrated: Tidbit loggers have a reported accuracy of 0.21 °C and a stability (drift) of 0.1 °C per year (<http://www.onsetcomp.com/products/data-loggers/utbi-001>) and iButtons have an accuracy of 0.5 °C (<https://datasheets.maximintegrated.com/en/ds/DS1922L-DS1922T.pdf>); the drift is reported by the manufacturer to be negligible, especially when compared to the ~2 °C accuracy of the biomimetic loggers (see *Technical Validation* below). Because of loss due to waves, each logger was typically used for only 2–3 years. Details on logger designs and field tests are described in detail in previous publications^{44,45,53}. In brief, logger thermal characteristics were calculated using empirical measurements of shell and tissue mass against length from adult *Mytilus californianus* collected on the west coast of North America. In addition to morphology (which determines convective heat flux) and colour (which affects solar heat load), the primary consideration is the maintenance of thermal inertia (the tendency of an object to resist temperature change as a function of external forcing). Mass/length relationships were combined with measurements of the specific heat capacity of shell and tissue to estimate total thermal inertia as a function of size⁴⁵. This was then compared to the thermal mass of polyester resin mussels of different lengths. The point where the two curves intersect is ~8 cm shell length; this was the size of the epoxy loggers. Silicone molds were cast from a representative 8 cm mussel, and were in turn used to pour two-part polyester resin (Evercoat) around the commercial Tidbit logger.

In some cases, iButton loggers were encased in ~8 cm mussel shells filled with silicone, which has a mass-specific heat similar to that of water. Comparisons of these instruments against adjacent mussels showed that silicone-filled shells recorded temperatures within ~1 °C of living animals⁵⁴. However, these loggers were considerably less durable and required more frequent maintenance (~bimonthly) than epoxy mussels (every 6–10 months), and so were used only infrequently at most sites. At some sites where the targeted mussel species is smaller (e.g., *M. edulis* in the Gulf of Maine), we used 4 cm mussel shells. Loggers of differing size were never used at the same site, and are distinguished from one another in the database. Nevertheless, any direct comparison between data collected by loggers of different sizes should be made with caution, as size can affect mussel temperature by several degrees⁵⁵.

Robomussels were deployed primarily on hard rock substrate, in growth position (posterior upward) in intact beds using Z-spar splash zone epoxy putty (Fig. 1). Care was taken to ensure that the logger was completely surrounded by other mussels, as tests showed that loggers deployed as solitary individuals tended to yield anomalously high readings. On the east coast of North America, loggers were also deployed at soft sediment (marsh) sites in mud substrate by attaching the loggers to dowel rod.

Deployment began in 1998 at the Hopkins Marine Station in Pacific Grove, California⁵⁴, and was expanded to other sites beginning in 2000 (Table 1 (available online only), Fig. 2). Total deployment time varied by location, ranging from less than a year to almost 18 years (average deployment time of 4 years). The number of loggers deployed and lost due to wave dislodgement also varied at each site, but a standard protocol was to deploy at least 3 loggers in the middle of mussel beds on horizontal, unshaded surfaces. At most sites, loggers were deployed at the upper edge of the mussel bed (‘upper’), half way between the upper and mid levels (‘upper mid’), mid level (‘mid’), half way between the mid and lower edge of the bed (‘lower mid’) and at the bottom of the mussel bed (‘lower’).

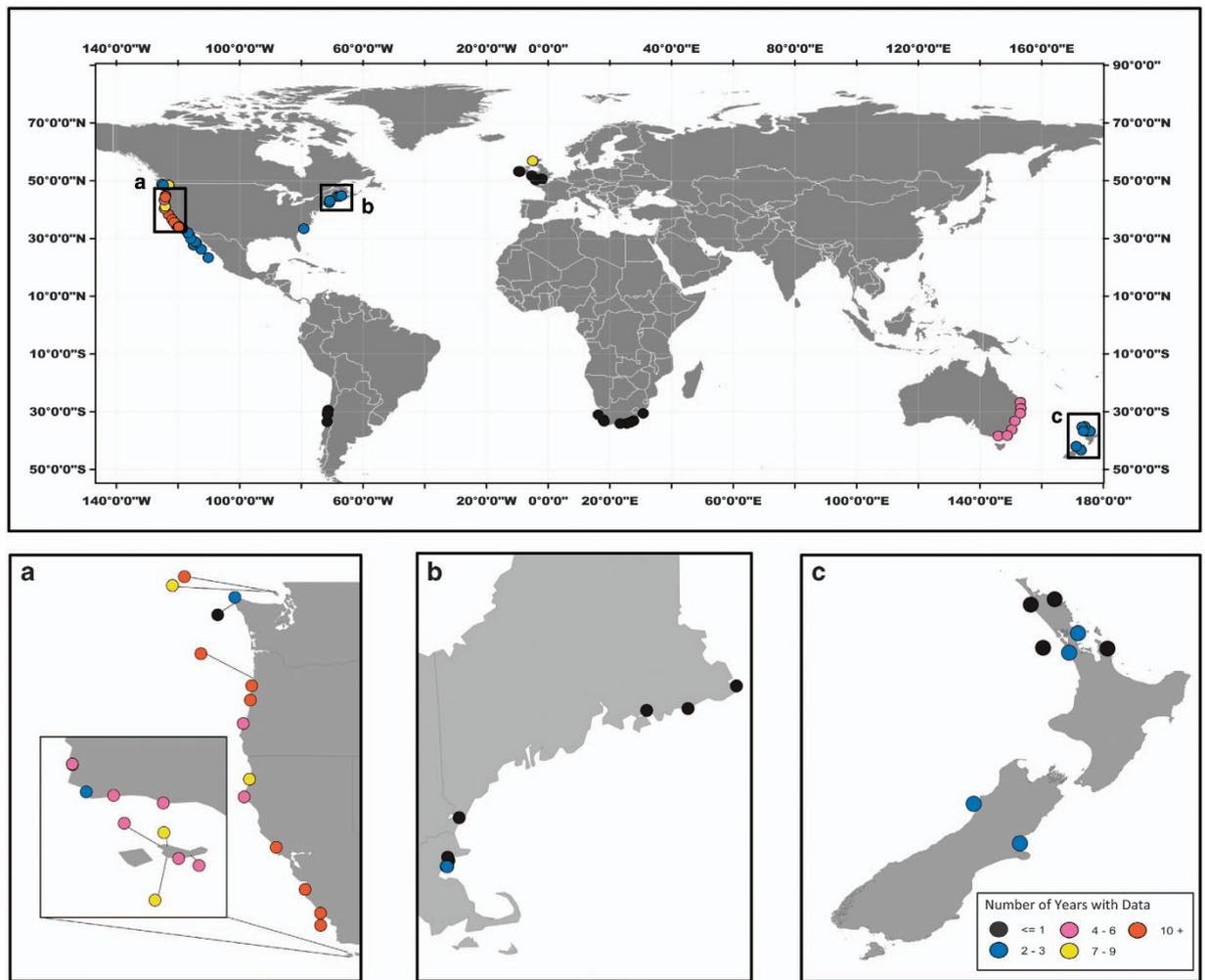


Figure 2. Map of logger deployment sites. Colors indicate approximate length of deployment, which ranged from one or two seasons to almost 18 years. Insets show (a) West and (b) East coasts of the United States and (c) New Zealand.

Loggers were programmed to record at intervals of 10–30 min and left in the field for periods up to 9 months before they were removed for downloading, and replaced with another logger. Every effort was made to place this new logger in precisely the same position in the bed as the logger being retrieved. All logger clock times were set to GMT. In the U.S., the absolute tidal elevation (height above chart datum) was measured with a Trimble R8 GNSS GPS system capable of sub-cm resolution. Temperature records were also used to record wave swash by comparing sudden drops in temperature (an indication of first wave splash following exposure at low tide) against predicted tidal elevations. The measurements of ‘Effective Shore Level’ can subsequently be compared against buoy records of significant wave height in order to estimate wave splash as a function of nearshore wave height at each site^{56,57}.

Code availability

Code written in R⁵⁸ was used to trim data recorded by each logger before and after deployment. A separate software program (SiteParser) is also available on the Northeastern website to determine the incidence of wave splash^{56,57}. This is accomplished by comparing rapid (user-defined) drops in temperature, indicative of the return of the tide, against predicted (Xtide software, www.flaterco.com/xtide) or measured (tidesandcurrents.noaa.gov) tide height for each site. By comparing these measurements against measured logger tidal elevations, it is possible to calculate the ‘effective shore level’ of a logger as a function of nearshore wave height⁵⁶. This also provides a method of dividing logger temperatures into aerial and submerged records. Notably, the choice of temperature drop determines both the accuracy of the division between aerial and submerged records, as well as the total amount of data available. Specifically, the choice of a larger temperature drop tends to increase certainty as to temperature divisions, but can restrict the amount of data to days when such drops are observed. For this

Parameter	Description	Unit
Logger type	Type of biomimic or logger	Text
Site Code	6-character site identification code (1st 2-characters: country; 2nd 2-characters: state; 3rd 2-characters: site)	Text
Site Name	Name of the site	Text
Region	Name of the region or jurisdiction	Text
Country	Name of the country	Text
Latitude	Latitude of the site	Decimal degree
Longitude	Longitude of the site	Decimal degree
Zone	Intertidal zone (low, lower mid, mid, upper-mid, upper)	Text
Substrate	Additional characteristics: muddy intertidal, rocky intertidal	Text
Wave Exposure	Wave exposure of logger (exposed or protected)	Text

Table 2. Data descriptors.

reason, the database provides data that have not been analyzed in this manner, but instead provides tools

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Back to Helmuth lab Home Metadata Readme Site Parser Tool Upload data Log out

DATABASE

fields marked with * are required

Help

Logger Type: * 8cm epoxy robomussel Country Name: * USA Region Name: * Oregon Site Name: * Strawberry Hill

Zone Name: * 3.mid Substrate: * Rocky Wave Exposure: * Exposed

Statistics: Max Temperature Frequency: per Day

2,836,681 Records Found
Min. Date Range: Mon, 22 May 2000 17:30:00 GMT
Max. Date Range: Tue, 20 Jan 2015 15:20:00 GMT

Filter by Date Range

Start Date Range: MM/DD/YYYY End Date Range: MM/DD/YYYY

Submit

Figure 3. Northeastern database showing dropdown menus. Users select Biomimic type (e.g., 8 cm epoxy logger); Country and Region (e.g., state); Site name; Intertidal zone (e.g., upper, mid, lower); Substrate type; Wave exposure, and Data statistic (raw, mean, maximum, or minimum over ranges of daily, monthly or yearly).

for the user to do so. A link to the open source SiteParser software program is provided on the Northeastern database website, along with links to all metadata including (when available) logger elevations.

Data Records

Data from all loggers are archived in two databases. The first is a searchable database maintained by Northeastern University (www.northeastern.edu/helmuthlab/Research/Database.html) and provides unrestricted access to data as well as to associated links such as the SiteParser software described above. Metadata for each microsite are included as a downloadable spreadsheet, which includes, for each site: Country, Region, Site name, and GPS coordinates (Table 1 (available online only)). The metadata file also includes information specific to each microsite, including: Biomimic logger type (unmodified ibutton, unmodified TidBit, epoxy [8 cm] mussel logger, shell (silicone-filled) mussel logger [4 or 8 cm length]), Substrate (rocky, muddy, tidepool), Tidal elevation zone (low, lower mid, mid, upper mid, or upper), Wave exposure (protected or exposed), and Start and end dates (Table 2). At the Northeastern website, data can be viewed and downloaded using a series of drop-down menus (Fig. 3). Given the range of selections, the database provides the range of dates over which data meeting those criteria are available (this information is also included in the metadata file). Data from each logger can be downloaded as raw data, as well as daily, monthly or annual maxima, minima and averages. Note that data include both aerial and submerged temperatures, but raw data can be parsed using the software provided. In instances

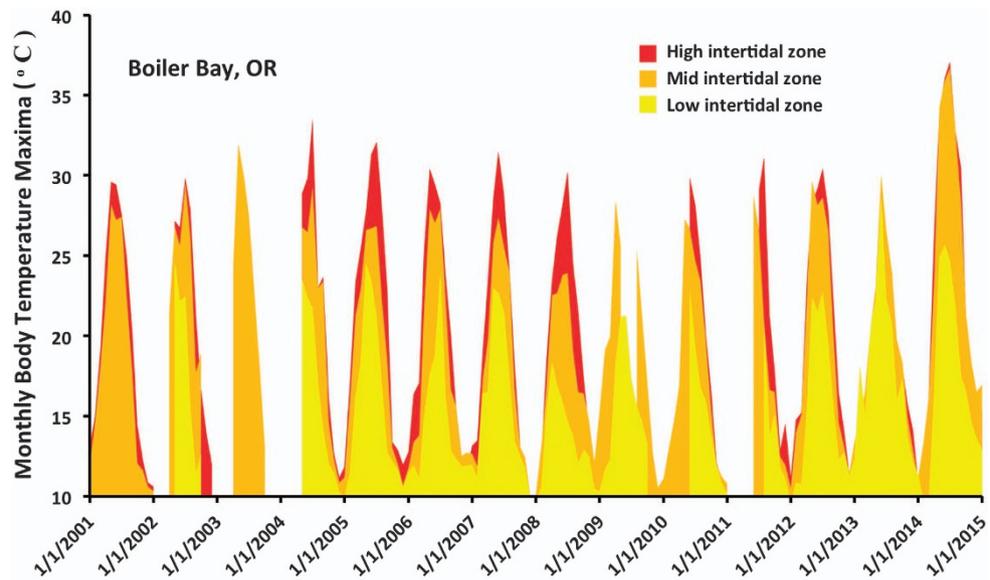


Figure 4. Monthly average daily maximum temperature at low, mid and upper intertidal elevations at a relatively wave-protected bench in Boiler Bay, Oregon.

where multiple microsites meet the selected criteria, the program takes the average at each time point from the maximum number of loggers available before calculating summary statistics. Data from all microsites can be downloaded as raw data to avoid this averaging procedure.

Raw data in text file format as well as associated metadata are also archived in a public repository (Data Citation 1). Files are organized in to a series of subfolders organized by Country, Region and Site (Table 1 (available online only)). Metadata identical to those available at the Northeastern site are also included as a downloadable file. Each data file contains information specific to the microsite in its header, and follows a 10 letter/6 number naming convention as follows: BM (indicating biomimetic logger database); Logger type (RM for mussel loggers [‘Robomussels’] or RB for unmodified loggers [‘Robobarnacles’]); 6 letter site code (Table 1 (available online only)); Country, Region, Site); two-digit microsite ID and four digit Year.

Technical Validation

Comparisons of logger temperatures against tissue temperatures of adjacent live mussels made using thermocouples are presented in four publications^{44,45,54,59}. The first compared temperatures recorded by a thermistor with the tip embedded in a silicone-filled shell against point measurements made from adjacent mussels in the field in Pacific Grove, California and found an average difference of $\sim 0.75^\circ\text{C}$ (ref. 54). The second involved a more comprehensive set of tests of epoxy (polyester) loggers in both the field and in a wind tunnel fitted with a heat lamp⁴⁵. In the laboratory experiments, the average difference between loggers and live mussels in artificial beds was $\sim 2.2^\circ\text{C}$ (ref. 45). Notably, the average difference between live mussels and unmodified loggers (TidbiTs) in the same experiment was 14.6°C . Field-tests yielded similar results, with an average error of 2.7°C between robomussels and live mussels⁴⁵. A follow-up study with additional laboratory tests over a wider range of temperatures ($10\text{--}50^\circ\text{C}$) reported a Root Mean Square Error (RMSE) of 3.84°C with a correlation coefficient of 0.89 between loggers and live mussels, with a bias of 0.8°C where loggers tended to overestimate temperatures slightly under extreme conditions⁴⁴. Finally, iButton loggers placed in the middle of silicone-filled *Geukensia demissa* shells were tested in a wind tunnel in artificial beds under a range of wind speeds; results showed average differences of $\sim 1.0\text{--}1.5^\circ\text{C}$ (ref. 59).

Usage Notes

Portions of the logger data presented here have been used in multiple field studies, and have provided context for laboratory studies. At small scales, biomimetic loggers (both loggers that we deployed as well as similar loggers made by other researchers) have been used to record differences in temperature among microhabitats (shaded and unshaded surfaces) and tidal elevations (Fig. 4) and the results compared to measurements of biochemical indicators of stress such as heat shock proteins^{54,60}, gene expression⁶¹, reproductive condition⁶², and to the fine-scale distribution of native and non-native species⁶³. At biogeographic scales, robomussels have been used to document thermal mosaics across large latitudinal gradients^{40,48} (Fig. 5) and the results related to patterns of mortality⁶⁴, physiological stress^{65–67} and growth^{68,69}, as well as interspecific differences in physiological stress³⁹ and geographic distribution⁷⁰.

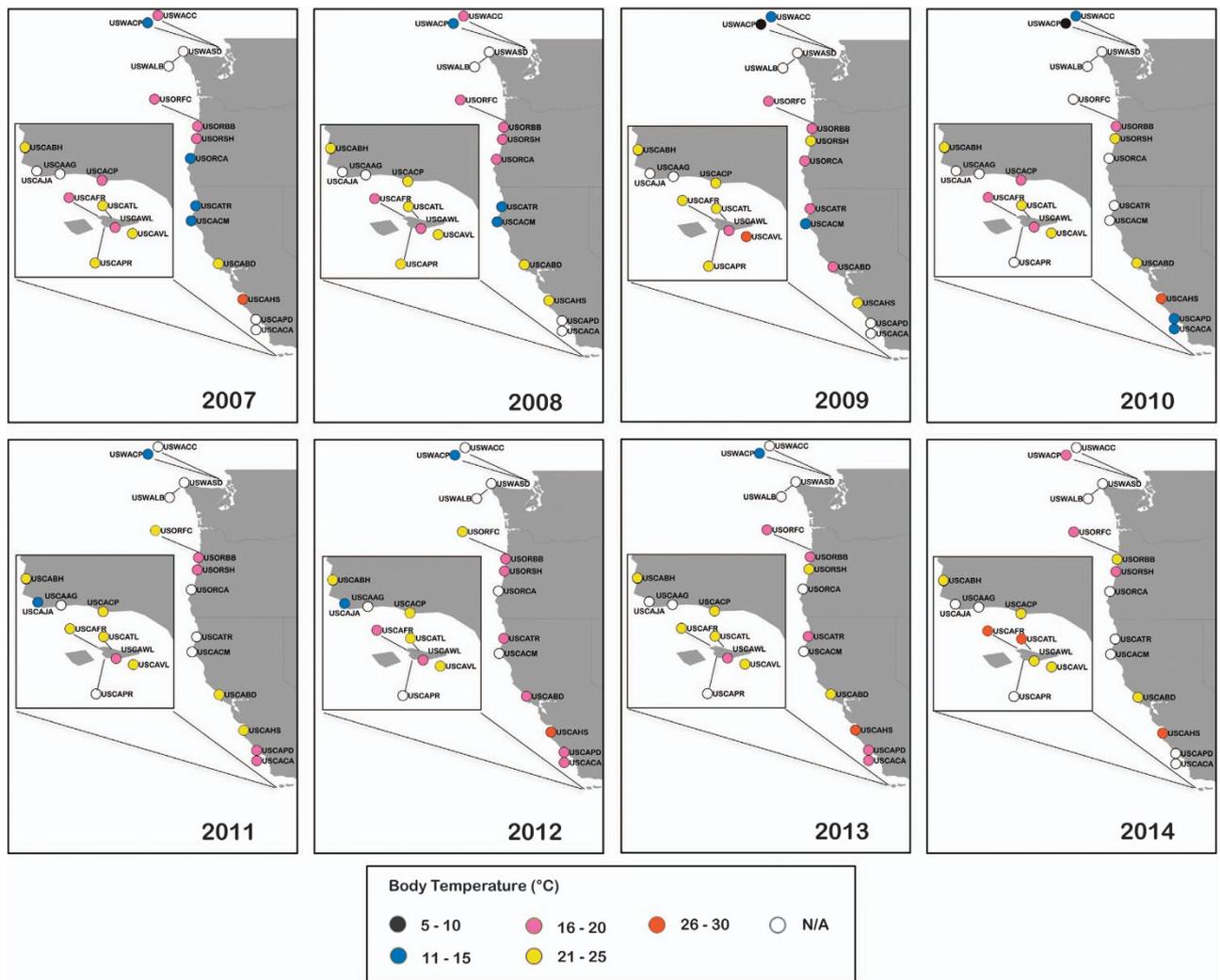


Figure 5. Monthly average daily maximum temperature (for the hottest month of each year at each site) at mid-intertidal elevations along the west coast of the United States (2007–2014).

Measurements from mussel biomimetics have been used to test heat budget models that estimate animal temperature using data from weather stations and satellites^{71–73}. Robomussels have also been used as part of controlled laboratory experiments that strive to replicate realistic field conditions^{37,74}. Finally robomussel data can be used to estimate wave splash and water temperature^{56,57}, although in this regard they do not present a major advantage over unmodified loggers.

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Data Citation

1. Helmuth, B. *et al.* *Dryad* <http://dx.doi.org/10.5061/dryad.6n8kf> (2016).

Acknowledgements

The collection of robomussel data has primarily been supported by grants from NSF (IBN-9985878, OCE-0323364, OCE-0926581 and IBN-1557868); NASA (NNG04GE43G, NNX07AF20G, NNX11AP77G), NOAA (NA04NOS4780264), the National Geographic Society to B.H., N.S.F. IBN-1557868 to B.H. and M.Z., and the David and Lucile Packard Foundation to PISCO, the Partnership for Interdisciplinary Studies of Coastal Oceans (B.M., G.E.H., C.B.) and by the Chilean Ministry of Economics (MINECON NC120086) to B.B. This work includes research supported by the South African Research Chairs Initiative of the Department of Science and Technology and the National Research Foundation (C.D.M.). This is publication number 468 of the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) and 343 of the Marine Science Center, Northeastern University. Numerous people helped to collect loggers over the last 18 years, and we are very grateful for their help: Tameka Breland, Susan Bolte, Nick Burnett, Cari Cardoni, Ryan Craig, Sean Craig, Colette Dryden, Tara Fitzhenry, Kristi Gardner, Shawn Gerrity, Chris Haas, Steven Hawkins, Maxine Henry, Lindsay Hunter, Scott Johnson, Nicole Kish, Ruth Milston-Clements, Gayle Murphy, Tom O'Keefe, Susanne Pender, Cathy Pfister, Camryn Pennington, Brittany Poirson, Sylvain Pincebourde, Eric Sanford and Morgan Timmerman-Helmuth. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of any of the authors' institutions or agencies.

Author Contributions

Helmuth led the study for the entire duration of the record. Logistics of deployment, retrieval and data management were, at various times, overseen by Choi, Matzelle, Szathmary, Gilman, Mislán, Yamane, Tockstein and Strickland. All other authors managed instrument deployment and retrieval at field sites: Massachusetts (Choi, Torossian, Morello); Scotland (Burrows); Ireland (Power, Gosling); U.K. (Hilbish, Mieszkowska); British Columbia and Washington (Nishizaki, Carrington, Harley); Oregon (Menge, Petes, Foley, Johnson, Poole, Noble, Richmond, Robart, Robinson, Sapp); California (Denny, Mach,

Miller, O'Donnell, Sones, Hilbish, Harley, Hofmann, Zippay, Blanchette, Macfarlan); Baja California (Carpizo-Ituarte, Ruttenberg, Peña Mejía); Chile (Broitman); New Zealand (Mislán, Petes, Ross, Menge) and South Africa (McQuaid, Lathlean, Monaco, Nicastro, Zardi). Helmuth led the writing of the manuscript and all authors contributed to editing.

Additional Information

Table 1 is only available in the online version of this paper.

Competing financial interests: The authors declare no competing financial interests.

How to cite this article: Helmuth, B. *et al.* Long-term, high frequency *in situ* measurements of intertidal mussel bed temperatures using biomimetic sensors. *Sci. Data* 3:160087 doi: 10.1038/sdata.2016.87 (2016).



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