LIMNOLOGY
and
OCEANOGRAPHY: METHODS

Limnol. Oceanogr.: Methods 7, 2009, 347–353

Robolimpets: measuring intertidal body temperatures using biomimetic loggers

Fernando P. Lima[1,2] and David S. Wethey[1]*

[1]Department of Biological Sciences, University of South Carolina, Columbia, SC, USA

[2]CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Vairão, Portugal

Abstract

This work introduces new biomimetic devices to record body temperatures of sessile intertidal animals. These waterproof devices, built around dissected circuit boards from Maxim DS1922 Thermochron iButtons, are demonstrated using intertidal limpets (*Tectura persona*). Data were validated by a field experiment carried out at Friday Harbor, Washington, USA. These loggers, named robolimpets, can easily be deployed to autonomously and accurately measure temperatures for long periods of time. Given that they mimic the visual aspect of real animals, they have the advantage of being inconspicuous in the intertidal environment. Their measurements not only match the temperature trajectories, but also the warming and cooling rates and daily temperature maxima and minima of live limpets. Robolimpets provide valuable data on the body temperatures experienced by intertidal animals.

Introduction

Warming of the world climate is unequivocal, and the recent increase in temperature has been regarded as a major driver of change in natural systems (Rosenzweig et al. 2007). In the intertidal zone, a physically severe and varying environment, temperature is probably the most important abiotic determinant of organismal performance and distribution from micro- to macroscales (Southward 1958; Crisp 1964; Lewis 1964; Southward 1995; Denny and Wethey 2000; Helmuth and Hofmann 2001; Wethey 2002; Gilman et al. 2006; Wethey and Woodin 2008). Nonetheless, because the capability to measure body temperatures experienced under field conditions is still largely undeveloped, indirect, remotely sensed, or even modeled environmental variables (such as the air or the sea temperature) are frequently used as surrogates for true body temperatures (e.g., Lima et al. 2006, 2007). This is problematic given that often temperatures experienced by these organisms are markedly distinct from the surrounding environment (Helmuth and Hofmann 2001). Miniaturized sensors and loggers that mimic the thermal characteristics of sessile intertidal species offer the opportunity to obtain thousands of organismal temperature records over the range of microhabitats occupied by these organisms. Equally important is the ability to measure environments where these organisms naturally do not occur. These geographical limits or gaps in distribution (at scales of meters or thousands of kilometers) are extremely informative to understand the biogeographic patterns or the physiological requirements of a given species (Wethey 2002; Lima et al. 2006). Taking measurements of body temperatures in areas where the species does not occur is obviously problematic. Biomimetic sensors/loggers are a relatively easy way to overcome this problem and still measure temperatures that closely resemble those experienced by real organisms. They potentially allow building large-scale networks of sensors, obtaining fundamental data for ecological, physiological, biogeographical, or even climate-monitoring studies.

Although recent advances in electronics have allowed the manufacture of increasingly smaller electronic components, the majority of temperature loggers commercially available are still too large for most ecological applications. For example, Onset Corporation Tidbit loggers, widely used for measuring intertidal organismal temperatures in the west coast of the United States (e.g., Helmuth and Hofmann 2001; Helmuth et al. 2002; Fitzhenry et al. 2004), can be modified to mimic only relatively large animals such as California mussels *(Mytilus*

*Corresponding author: E-mail: fplima@biol.sc.edu

Acknowledgments

The authors thank Jerry Hilbish, Brian Helmuth, Sarah Woodin, and Sierra Jones for the insightful conversations that resulted in design improvements. This study was funded by NOAA Ecological Forecasting (NA04NOS4780264), NASA Earth Science Enterprise (NNG04GE43G), and NASA (NNX07AF20G). F.P.L. was also supported by a FCT grant (SFRH/BPD/34932/2007). Arthur Illingworth and Allen Frye designed and built the underwater housing for the Campbell CR10X data logger. Limpet shell drawing by A. L. Araújo. The Friday Harbor Laboratories of the University of Washington provided laboratory space.

californianus). That excludes nearly all the remaining intertidal mussel species, barnacles, and limpets. Therefore, not only is the application of such large loggers limited to a handful of species, but the geographical area potentially sampled by this method is roughly restricted to the geographic range of those few species. On the other hand, iButton Thermochron temperature loggers (DS1921, Maxim Integrated Products) have much smaller dimensions and, although not designed to be waterproof, have been successfully used in intertidal and subtidal environments (e.g., Wethey 2002; Harley and Helmuth 2003; Harley and Lopez 2003; Dale and Miller 2007). Their main disadvantages are the limited memory that only stores 2048 readings and a resolution of 0.5°C, which is insufficient for many applications. Unfortunately, the high-resolution iButton Thermochron (Maxim DS1922, capable of storing 8192 readings) has a much weaker casing seal, and thus the loss rate due to seawater leaks makes the extensive use of these loggers not viable (F. P. Lima, unpublished data). Simply protecting the logger by embedding it in a case or cast is impracticable since its programming and data downloading requires physical contact by an external reader. WeeTag Lite miniaturized temperature loggers (α Mach) offer higher memory (capable of storing 32,000 values) and a better resolution (0.025°C) in a package with a size equivalent to iButtons, but have other disadvantages. They are two to three times more expensive, have less powerful batteries, and also require contact by an external reader, making them unsuitable for hard-embedded applications.

This study describes a new type of self-contained, rugged, and miniaturized temperature sensor/logger that can be easily and inexpensively built and used to mimic the thermal characteristics of a suite of sessile intertidal organisms and record their thermal trajectories over a broad variety of temporal and spatial scales. Besides coping with the above problems, the new kind of sensor also mimics the visual aspect of real animals, being inconspicuous in the intertidal environment and thus being unlikely to be intentionally destroyed, which may be a major problem in long-term studies deploying eye-catching devices (F. P. Lima, unpublished data). To demonstrate the new method, data on the validation of the sensors mimicking limpets (called robolimpets) is presented. Robolimpets were deployed for a week at an intertidal rocky shore in San Juan Island, Washington, USA, and their readings were validated by comparison with temperatures experienced by live animals.

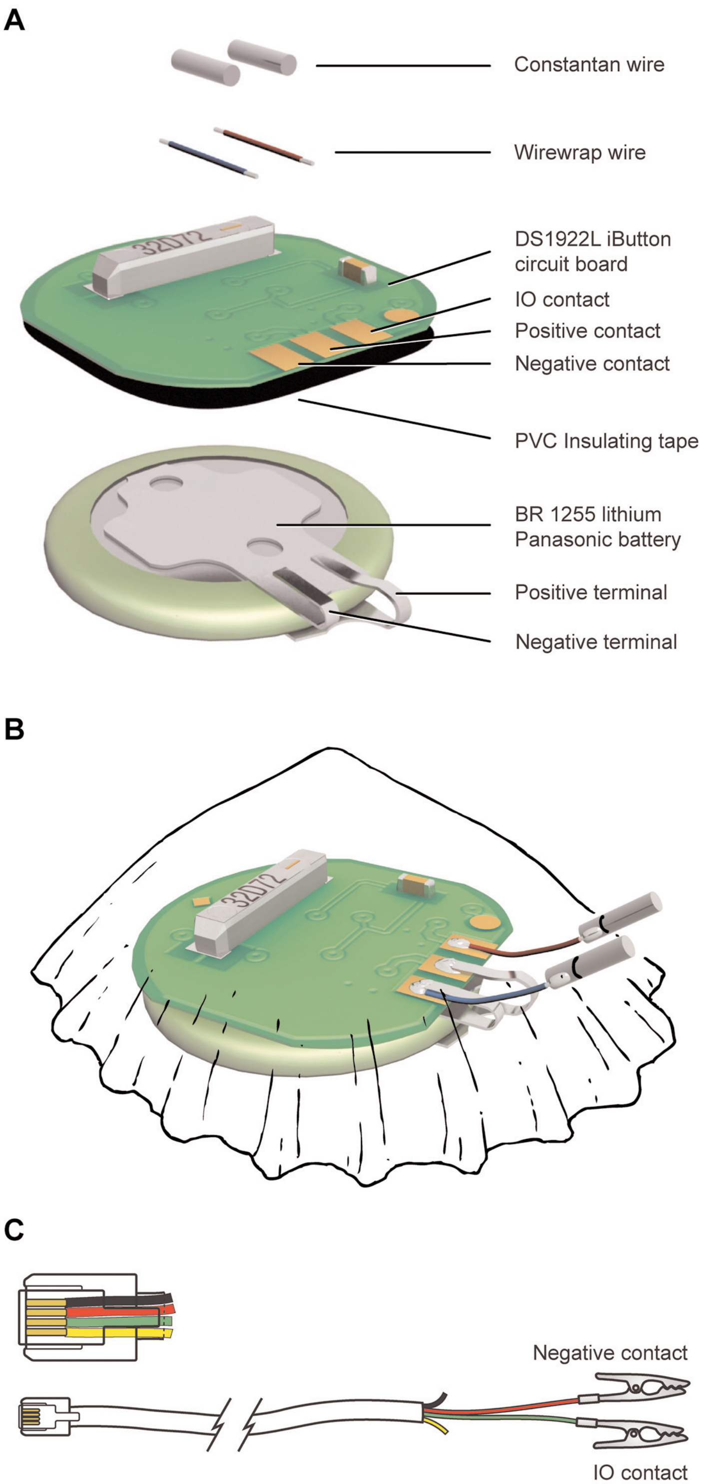


Fig. 1. (A) Exploded view of the different parts used for robolimpet assembly. (B) Schematic view of the assembled electronics inside a limpet shell. (C) Wiring for the connection cable to service robolimpets.

Materials and procedures

Logger construction—Robolimpets consist of a lithium battery powering the circuit board from a DS1922 iButton, embedded in a waterproof compound, inside an emptied real limpet shell (see Fig. 1). Two exposed wires penetrating the shell serve as contacts for logger programming and subsequent data retrieval. The DS1922 iButton hardware can be programmed to record up to 8192 readings at 0.5°C or 4096 readings at 0.0625°C resolution, measured at intervals from 1 s to 273 h, with an accuracy of ± 0.5°C (Dallas 2007).

The first step in robolimpet assembly involves dissecting or dehousing a DS1922 iButton. This is an opportunity to recycle old and even nonworking, corroded iButtons, since the circuit board often remains perfectly functional despite all the other parts having gone bad. iButtons have a stainless steel case that can be cut open with the help of a Dremel Rotary Tool fitted with a abrasive cutting wheel (Dremel part 420). The internal architecture of DS1922 iButtons makes them very susceptible to damage by vertical compression. Thus, they should be held laterally with locking pliers (see Fig. 2), which are firmly held in a vise. The use of a rotary power tool, in contrast with a manual hacksaw, permits a clean and rapid cut, reducing the probability of internal damage. Two or three vertical cuts are enough to allow the casing to be opened (like a banana, viz. Robert and Thompson 2003) and pulled apart with a pair of needlenose pliers. The circuit board is then separated from the battery clip, thoroughly washed with water, and dried with isopropanol.

The original coin type lithium battery (3V, 40 mAh) may be kept or may be replaced by a higher-capacity one. The use of fresh batteries is essential when recycling old loggers. A Panasonic BR1255-1VC battery (3V, 48 mAh, Digikey, part P192-ND) was preferred due to its high capacity and small dimensions (12.5 × 2.00 mm). The battery terminals were cut and bent until they matched the circuit board terminals, respecting the correct polarity (see Fig. 1). The side of the circuit board facing the battery was covered with PVC insulating tape to prevent short circuits. The dimensions of the coupled circuit board/battery did not exceed 14 by 4 mm, weighing approximately 1.5 g. Two pieces of AWG 30 wirewrap wire (Digikey part K329-ND) were soldered to the appropriate terminals, connecting the circuit board to the outside contacts in the shell. This wire is extremely flexible and easily bent inside the limpet shell. The external contacts were made of 1.6-mm-diameter constantan thermocouple wire (part EXPP-T-14, Omega Engineering), which is not affected by saltwater corrosion. These contacts were passed through 1.6-mm-diameter holes that were drilled into the shell using a Dremel Rotary Tool fitted with a high-speed cutter (Dremel part 569). Shells from live animals (*Tectura persona*) were obtained by killing limpets by quick immersion in boiling water. Shells were then thoroughly cleaned with dishwashing liquid. Limpets 20–35 mm in length were chosen because that was the smallest size that could easily accommodate the necessary electronic parts.

One of the main concerns when building biomimetic sensors/loggers is to choose a combination of materials yielding thermal properties equivalent to those exhibited by living organisms (Helmuth 2002; Fitzhenry et al. 2004). For the robolimpet loggers, the part that probably contributes most to the average specific heat of the device (therefore significantly determining the warming and cooling rates) is the material that fills the shell and waterproofs the electronics. Preliminary trials were done under controlled laboratory conditions, exploring a variety of materials and selecting those with promising thermal characteristics for further trials in the field. Two different materials were finally selected: (*a*) A-788 Z-Spar Splash Zone Compound (Kopper's Company), hereafter referred to as Z-Spar, and (*b*) 3M Scotchcast 2130 Flame Retardant Compound, hereafter referred to as Scotchcast 2130. Ten robolimpets were built, five with each material. Each compound is obtained as two separate liquid parts that must be mixed to polymerize. The mixture was poured into shells previously fitted with the electronic parts and was allowed to fully harden for at least 24 h before deployment. All electronic parts, including the solder joints between the wirewrap wire and the constantan wire, were immersed in the waterproofing compound to prevent corrosion.

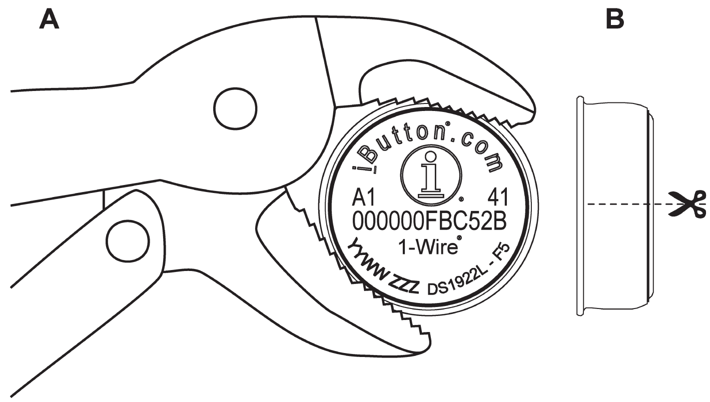


Fig. 2. (A) Thermochron iButton held laterally with locking pliers. (B) Representation of the vertical cuts used to open the iButton casing.

Connector cable assemblage—A data cable was made by stripping one end of a RJ-11 telephone cable and soldering two small alligator clips (Radio Shack, part 270-373) to the green and red wires (pins 3 and 4, respectively). These clips were then connected to the robolimpet's negative and IO external contacts, respectively (see Fig. 1C). The other end of the cable received a RJ-11 telephone connector to be used with the 1-wire USB iButton adapter (Maxim Integrated Products part DS9490R). Robolimpets were programmed in the field using OneWireViewer software (www.maxim-ic.com/products/ibutton/software/resources.cfm) with a laptop computer.

Assessment

We assessed the accuracy and usefulness of biomimetic loggers in measuring temperature patterns in the field by validating their recorded temperature trajectories against body temperatures of live limpets exposed to the same environmental conditions. Robolimpets were deployed close to living equivalents in a rocky shore at Friday Harbor, San Juan Island, Washington, USA (48°33.039′N, 123°00.335′W). In this region, limpets with adequate dimensions (20–35 mm in length) were found only on the upper fringe of the intertidal zone, usually in microsites with some degree of protection from excessive wave action and solar radiation. The study area was approximately 4 by 0.5 meters, lying approximately at 3.5 meters above the mean lower low water (MLLW) level in the base of a 60-degree slope, on an east-facing rocky surface.

A small hole was drilled on the shell of five numbered live limpets using a Dremel Rotary Tool fitted with a #108 engraving cutter drill bit. A thin copper-constantan thermocouple (Omega part TT-T-40-SLE) wire with a cross section of 0.16 mm was then inserted into the hole and sealed with Z-Spar. Temperatures were logged every 2 min using a Campbell Scientific CR10X logger (accuracy ±0.1°C) in a waterproof housing above the intertidal zone. Five robolimpets made with Z-Spar and five made with Scotchcast 2130 were deployed in the same area. Given that preliminary trials suggested a tight relation between the microhabitat occupied by the limpets and their patterns of body temperatures, one exemplar of each kind of robolimpet was deployed adjacent to each live animal with an inserted thermocouple probe. Robolimpets were glued to the rocky substrate using a thin layer of Z-Spar and were programmed to record temperatures every 2 min at 0.0625°C resolution. Data were downloaded, loggers were reset, and the wiring and position of each live limpet was checked every day. Although the average distance between each robolimpet and the nearest live neighbor was approximately 6 cm immediately after deployment, animals 1, 3, and 4 increased their distance from their corresponding robolimpet to 20, 45, and 15 cm during the first tide cycle period, probably because of the disturbance caused by handling and thermocouple probe insertion. After the first disturbance and during the rest of the field study, the position of the five limpets did not change noticeably. Data were collected for a period of 8 days (from May 26 to June 2, 2008), but the first 24 h of data were not used to allow full recovery of the live animals from handling.

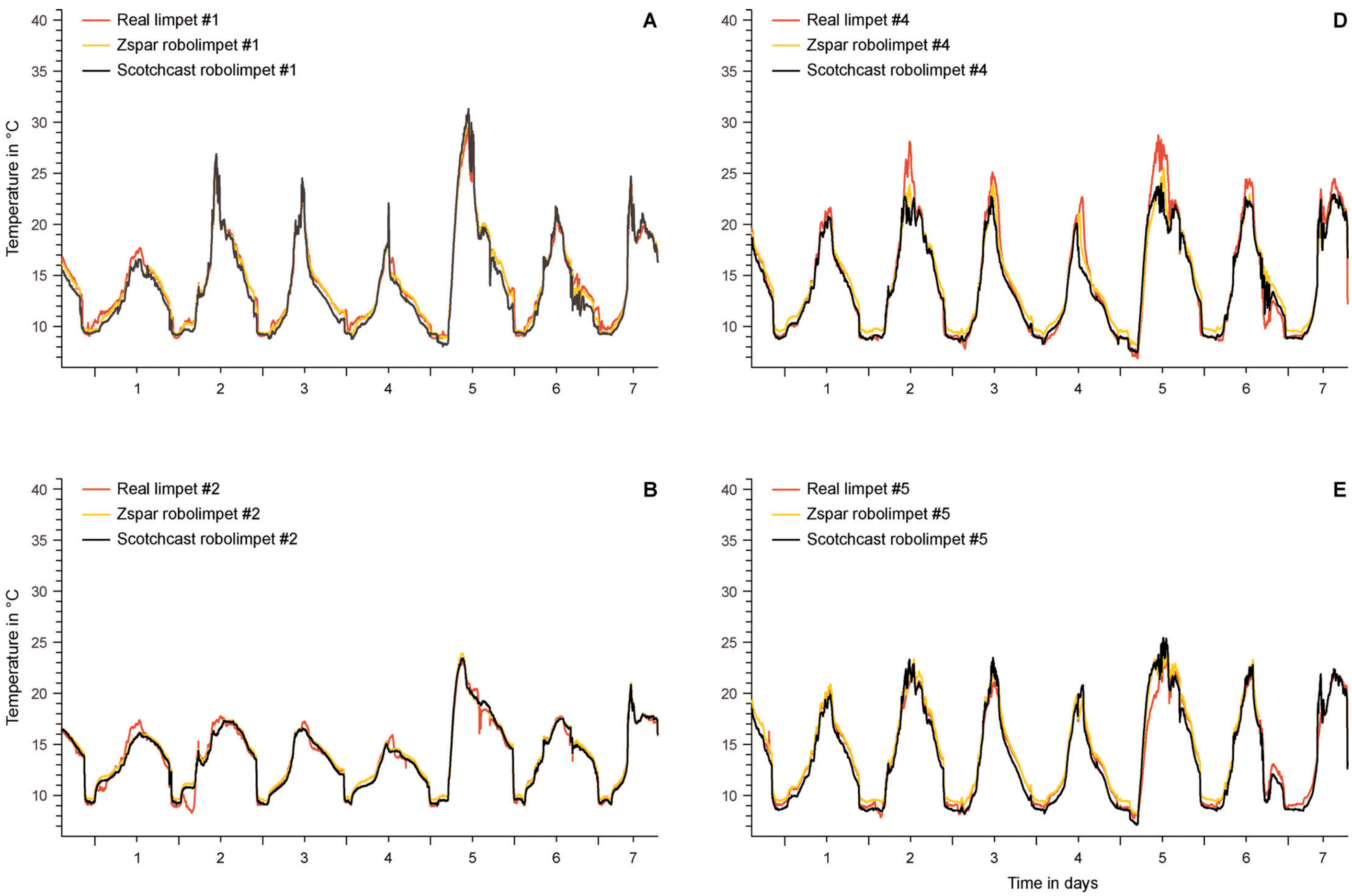
Trajectories of live limpet body temperatures and biomimetic logger temperatures are reported in Fig. 3. There is high natural variability among live animals, despite being within a few meters from each other, approximately at the same tidal height and in a rocky surface with the same general orientation in relation to the sun. Slight differences in surface topography and degree of shading from nearby rocks are responsible for these differences between individuals (e.g., Wethey 2002). The similarity between each robolimpet and its reference live limpet was remarkable (Fig. 3). Not only the maximum and minimum daily values (occurring during day and nighttime low tides, respectively) were very similar, but also the trajectories were synchronous. Equally important was the match between the warming and cooling rates of each live limpet and those recorded by robolimpets. The merits of biomimetic models in reproducing real limpet body temperatures are also portrayed in Table 1. As descriptors of the thermal trajectory of a given live limpet, robolimpets were shown to be as good as or better than other live animals in the surroundings. This can be seen from the root mean square deviation (RMS) statistics in Table 1. The average RMS deviation of individual live limpets from the mean of all limpets was 2.64°C, whereas the Z-Spar and Scotchcast robolimpets had RMS deviations of 0.87°C and 1.06°C, respectively, from their paired live limpets (Table 1). Loggers made of Z-Spar were always slightly better than models built with Scotchcast 2130. For example, correlations between robolimpets and their nearest limpets were on average 0.99 ± 0.01 for Z-Spar and 0.98 ± 0.01 for Scotchcast 2130, whereas among live limpets they were 0.91 ± 0.05 on average.

Although robolimpets filled with Z-Spar had slightly better thermal characteristics that those filled with Scotchcast 2130, they were more prone to leakage and failure in long deployments. An ongoing long-term experiment on the Iberian Peninsula shows that robolimpets built with Z-Spar are failing at a very high rate (75% in some cases) after 6 months of deployment, whereas those built with Scotchcast 2130 are much more resistant (less than 10% of loggers failed). Examination of nonworking loggers has shown that Z-Spar is prone to open microfissures and cracks with time, exposing the sensitive electronics to salt water, causing failure.

Robolimpets can be easily programmed and deployed (a single low tide gives enough time to deploy some dozens at a given location). At the end of the experiment, they can be recovered by breaking the Z-spar layer between the robolimpet and the substrate and redeployed at different locations. With the 48-mAh battery, and assuming a sampling rate of 48 samples per day, the battery life is expected to be more than 4 years of data collection (Dallas 2007). Loggers can be turned off when they are not being used in the field, lengthening total effective life span. Exhausted batteries are not replaceable, because after the Scotchcast 2130 has hardened it is almost impossible to remove electronic components without damage. Still, each biomimetic logger is expected to collect more than 60,000 measurements before the battery is depleted, which makes a good cost/benefit ratio since each logger costs approximately $50.

Discussion

This work demonstrates the utility of autonomous, biomimetic sensors/loggers in providing accurate data on the body temperatures experienced by intertidal animals. Although the present proof-of-concept focused specifically on building loggers similar to limpets (robolimpets), the same method can potentially be used to create a variety of loggers mimicking different intertidal animals such as mussels, oysters, dogwhelks, topshells, barnacles, and others. Until now, the alternative to record organismal temperatures of such small animals during both low and high tide involved inserting a thermocouple wire on the body of the animal. The probe was usually connected to a long cable running to a logger placed above the water level that had to be periodically serviced. Besides being very sensitive to damaging by waves and extreme weather, this design was impractical for large-scale studies, and it did not allow taking measurements in places where animals were absent. The technique presented here offers the potential to answer a large number of previously intractable questions, on an array of applications on intertidal ecology, invertebrate physiology,



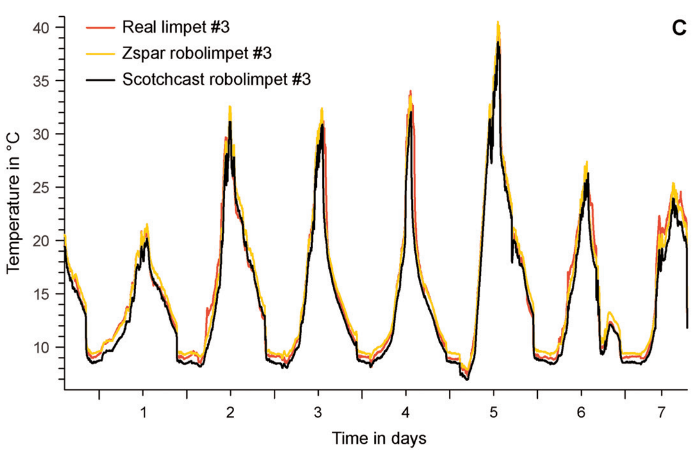


Fig. 3. Temperature trajectories for limpets 1, 2, 3, 4, and 5 and their corresponding robolimpets during the deployment period.

Table 1. Temperature trajectory comparisons among live limpets, between each live individual and the nearest Z-Spar robolimpet, and between each live individual and the nearest Scotchcast robolimpet.

	RMS	Corr	Bias
Among live	2.64 ± 1.00	0.910 ± 0.047	–0.10 ± 0.83
Zspar versus live	0.87 ± 0.36	0.998 ± 0.005	0.17 ± 0.22
Scotchcast versus live	1.06 ± 0.39	0.984 ± 0.005	–0.45 ± 0.32

RMS, mean root square error; Corr, average Pearson's correlation; Bias, average bias.

developmental biology, thermal pollution and stress, behavioral adaptations, biogeography, or even climate-monitoring studies. The low cost of the loggers, and their autonomy, means that it is possible to build large-scale networks of sensors to monitor the frequency distribution of stressful events through time. These data are critical to study the biological effects of global warming on the intertidal environment and to forecast expected changes under future climate scenarios.

The accuracy of robolimpets in measuring the thermal trajectory of each live limpet indicates that this methodology will be extremely useful for even small-scale and short-term assessments. Conversely, some caution must be taken when generalizing data logged by a single robolimpet to a larger extension of habitat. Ideally, a minimum number of loggers covering the totality of microhabitats within the study area should be deployed. This number will depend on the sample area and microtopography, but five is probably a minimum number. Another aspect that should not be disregarded is the potential size-specificity accuracy of the logger. Although preliminary trials have suggested that the effect of the logger size may be neglected in relation to the effect of the microhabitat where the logger is deployed (e.g., Fig. 3), extremely large or extremely small limpets were not tested at all, and thus the extent to which such modifications in logger design would affect the results is not known. For limpets, the relatively small influence of the logger/animal size on the attained temperatures may be explained by their shape, with a very large area in contact with the underlying rock, meaning that their temperatures are strongly affected by conductive heat transfer to and from the substratum (Helmuth 2002; Denny and Harley 2006). Also, for many limpet species, the shell color is in general much more similar to the rock color than the shells of other animals are (e.g., barnacles are usually lighter and mussels darker than the rock they inhabit). Thus, the degree of decoupling between the body and the substratum temperatures that was previously reported for large, dark mussels (Helmuth 2002) is probably much smaller in limpets. This is also in agreement with the observation that the material chosen to fill and waterproof the electronics had a smaller influence on the logged temperatures than it could be expected a priori.

Comments and recommendations

Robolimpets made with Z-Spar Splash Zone Compound had slightly better thermal characteristics than those filled with Scotchcast 2130 Flame Retardant Compound. However, 75% of Z-Spar loggers leaked during 6-month deployments, whereas Scotchcast 2130 loggers had only 10% failure rates. Z-Spar should not be used for waterproofing any electronic device in intertidal conditions for more than a few days. The material that has the best combination of thermal fidelity and durability is the Scotchcast 2130.

The miniaturization obtained by dissecting iButtons and repackaging the components allows the construction of a

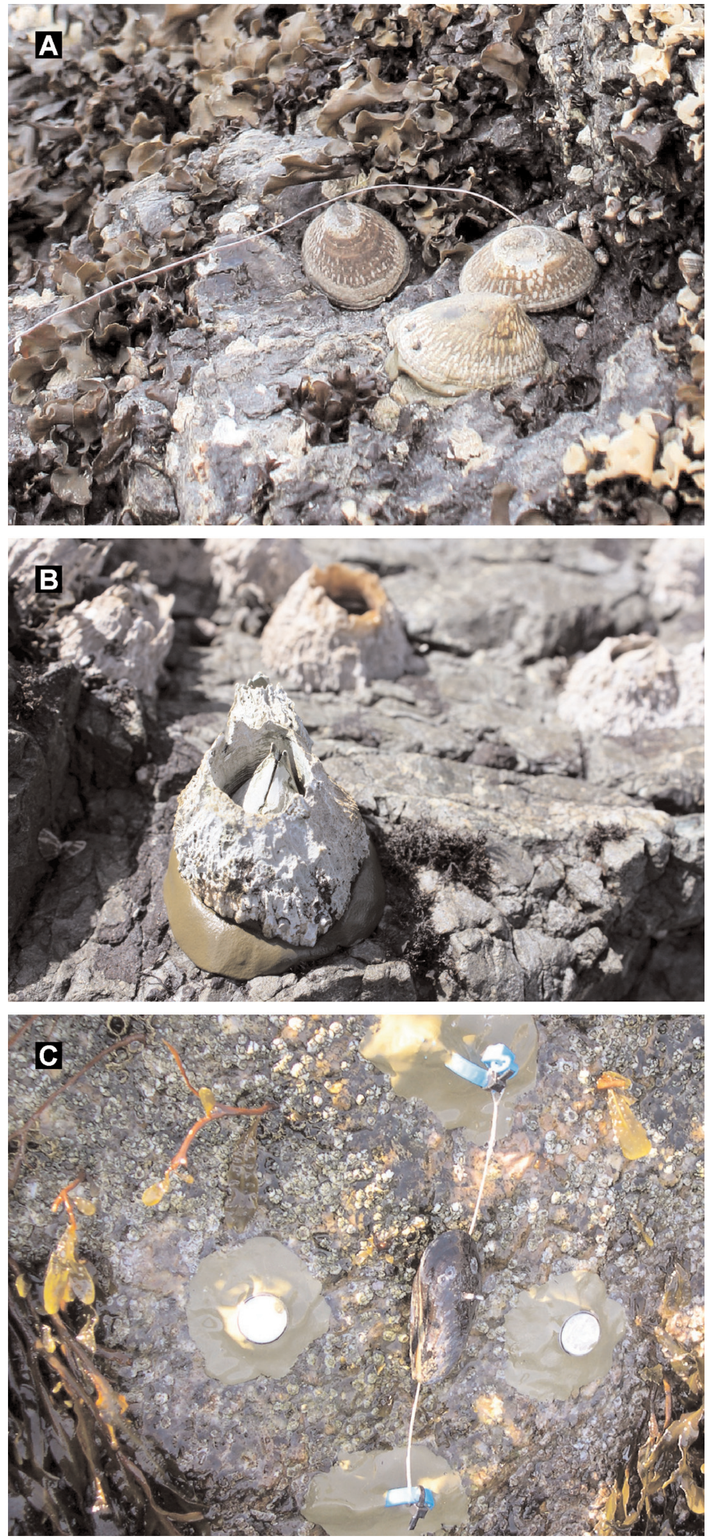


Fig. 4. Biomimetic loggers deployed in the field. (A) A robolimpet in the center, showing the two programming/data retrieving contacts, accompanied by two live animals (*Tectura persona*), on the right with a thermocouple probe inserted. (B) Robobarnacle (shell of *Semibalanus cariosus*), showing the two data contacts near the base. (C) Robomussel (shell of *Mytilus* spp.) deployed together with two unmodified iButtons.

great variety of biomimetic loggers for a diversity of intertidal animals. Besides showing a robolimpet deployed in the field, Fig. 4 depicts robobarnacles (*Semibalanus cariosus*) and robomussels (*Mytilus edulis* complex). For some species like barnacles, it is useful to glue the shell parts together before filling the interior volume with waterproof material. For robomussels, each valve was filled separately with Scotchcast 2130 (electronics were embedded in one of the sides) before gluing them together. To mimic the way each animal naturally attaches to the substratum, robobarnacles were glued using a small amount of Z-Spar Splash Zone Compound. Robomussels were constructed with an embedded stainless steel fishing leader wire; the wire was then attached to cable ties held by Z-Spar to the rock surface, thereby mimicking the byssus thread attachment mechanism of live mussels. Therefore, in the near future it may be possible to use a suite of different loggers to study how body temperatures are influenced by the interplay between the tides, the weather, the microhabitat, and the physical characteristics of the animals (such as the shell material, color, and shape) on a wide range of intertidal species, over large geographic scales. It must be stressed, however, that the design of different kinds of loggers (mimicking different species such as bivalves) should be accompanied by laboratory or field assessments to evaluate how well those new designs resemble real-world body temperatures.

References

Crisp, D. J., Ed. 1964. The effects of the severe winter of 1962-63 on marine life in Britain. J. Anim. Ecol. 33:179-210.

Dale, R. K., and D. C. Miller. 2007. Spatial and temporal patterns of salinity and temperature at an intertidal groundwater seep. Estuar. Coast. Shelf Sci. 72:283-298.

Dallas. 2007. DS1922L, DS1922T data sheet. www.maxim-ic.com (accessed April 17, 2009).

Denny, M. W., and C. D. G. Harley. 2006. Hot limpets: predicting body temperature in a conductance-mediated thermal system. J. Exp. Biol. 209:2409-2419.

——— and D. S. Wethey. 2000. Physical processes that generate patterns in marine communities. *In* M. Bertness, S. Gaines and M. Hay [eds.] Marine Community Ecology. Sunderland, MA: Sinauer Associates, p. 1-37.

Fitzhenry, T., P. M. Halpin, and B. Helmuth. 2004. Testing the effects of wave exposure, site, and behavior on intertidal mussel body temperatures: applications and limits of temperature logger design. Mar. Biol. 145:339-349.

Gilman, S. E., D. S. Wethey, and B. Helmuth. 2006. Variation in the sensitivity of organismal body temperature to climate change over local and geographic scales. Proc. Nat. Acad. Sci. U.S.A. 103:9560–9565.

Harley, C. D. G., and B. S. T. Helmuth. 2003. Local- and regional-scale effects of wave exposure, thermal stress, and absolute versus effective shore level on patterns of intertidal zonation. Limnol. Oceanogr. 48:1498–1508.

——— and J. P. Lopez. 2003. The natural history, thermal physiology, and ecological impacts of intertidal mesopredators, *Oedoparena* spp. (Diptera: Dryomyzidae). Invertebr. Biol. 122:61-73.

Helmuth, B. 2002. How do we measure the environment? Linking intertidal thermal physiology and ecology through biophysics. Integr. Comp. Biol. 42:837-845.

———, C. D. Harley, P. M. Halpin, M. O'Donnell, G. E. Hofmann, and C. A. Blanchette. 2002. Climate change and latitudinal patterns of intertidal thermal stress. Science 298:1015-1017.

——— and G. E. Hofmann. 2001. Microhabitats, thermal heterogeneity and patterns of physiological stress in the rocky intertidal zone. Biol. Bull. 201:374–384.

Lewis, J. R. 1964. The Ecology of Rocky Shores. London: English University Press Ltd.

Lima, F. P., N. Queiroz, P. A. Ribeiro, S. J. Hawkins, and A. M. Santos. 2006. Recent changes in the distribution of a marine gastropod, *Patella rustica* Linnaeus, 1758, and their relationship to unusual climatic events. J. Biogeogr. 33:812-822.

———, P. A. Ribeiro, N. Queiroz, R. Xavier, P. Tarroso, S. J. Hawkins, and A. M. Santos. 2007. Modelling past and present geographical distribution of the marine gastropod *Patella rustica* as a tool for exploring responses to environmental change. Glob. Change Biol. 13:2065–2077.

Robert, K. A., and M. B. Thompson. 2003. Reconstructing Thermochron iButtons to reduce size and weight as a new technique in the study of small animal thermal biology. Herpetol. Rev. 34:130-132.

Rosenzweig, C., G. Casassa, D. J. Karoly, A. Imeson, C. Liu, A. Menzel, S. Rawlins, T. L. Root, B. Seguin, and P. Tryjanowski. 2007. Assessment of observed changes and responses in natural and managed systems, p. 79-131. In M. L. Parry, O. F. Canziani, J. P. Palutikof, and P.J. van der Linden [eds.], Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press.

Southward, A. J. 1958. Note on the temperature tolerance of some intertidal marine animals in relation to environmental temperatures and geographic distribution. J. Mar. Biol. Assoc. U.K. 37:49-66.

———. 1995. The importance of long time-series in understanding the variability of natural systems. Helgoländer Meeresuntersuchungen 49:329-333.

Wethey, D. S. 2002. Biogeography, competition, and microclimate: the barnacle *Chthamalus fragilis* in New England. Integr. Comp. Biol. 42: 872-880.

——— and S. Woodin. 2008. Ecological hindcasting of biogeographic responses to climate change in the European intertidal zone. Hydrobiologia 606:139-151.

Submitted 20 December 2008
Revised 20 February 2009
Accepted 19 March 2009