Near-daily reconstruction of tropical intertidal limpet life-history using secondary-ion mass spectrometry

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Measurements of life-history traits can reflect an organism’s response to environment. In wave-dominated rocky intertidal ecosystems, obtaining in-situ measurements of key grazing invertebrates are constrained by extreme conditions. Recent research demonstrates mollusc shells to be high-resolution sea-surface temperature proxies, as well as archival growth records. However, no prior molluscan climate proxy or life-history reconstruction has been demonstrated for the tropical rocky intertidal environment—a zone influenced by warmer waters, mixed tides, trade-wind patterns, and wave-action. Here, we show near-daily, spatiotemporal oxygen isotope signatures from the tropical rocky intertidal environment by coupling secondary ion mass spectrometry analysis of oxygen isotopes with the sclerochonology of an endemic Hawaiian intertidal limpet Cellana sandwicensis, that is a significant biocultural resource harvested for consumption. We also develop a method for reliable interpretation of seasonal growth patterns and longevity in limpets. This study provides a robust approach to explore tropical intertidal climatology and molluscan life-history.
Understanding the phenotypic plasticity of marine species to environmental change is crucial to understand the dynamics of coastal populations. Recent responses across multiple marine taxa to extreme sea surface temperature (SST) anomalies highlight the need for intertidal research focusing on thermal tolerance and habitat shifts. For rocky intertidal ecology, however, monitoring climate responses in-situ presents significant challenges under adverse tide-, wave-, and wind-exposed conditions; and sub-anually resolved oceanographic climate proxies have only recently been identified for this semi-terrestrial environment. Similar to other oceanographic climate proxies (i.e., coral skeletons, fish otoliths, foraminifera), most mollusc shell are precipitated in isotopic equilibrium with seawater. In these accretionary hard-tissues, oxygen isotopes ratio ($\delta^{18}O$) measurements can be aligned with physiochemical features to infer seasonality with more negative values reflecting warmer climate and more positive values reflecting cooler climate.

To date, robust reconstruction of seasonal to millennial sea-surface temperature (SST) from mollusc shells are numerous in mid-to-high latitudes—where $\delta^{18}O$ is strongly correlated with seawater temperature. In contrast, SST proxies in low latitudes are limited to subtidal organisms (primarily corals), as hydrological processes (i.e., rainfall, estuarain mixing) influencing sea surface salinity (SSS) can confound drivers of $\delta^{18}O$. Therefore, while corals are established long-term proxies of mean annual SST, a high-resolution proxy for tropical intertidal climate is missing entirely.

Mollusc limpet shells are an excellent candidate for tropical intertidal climate proxy records due to their archeological preservation, wide distribution, and sequential growth. With absolute temporal alignment of growth, ecologists can interpret species’ responses to physiological (i.e., ontogeny, reproduction) and environmental (i.e., extreme climate, tide) factors.

Within the Hawaiian Archipelago, endemic intertidal limpets (Cellana spp.) are a significant biocultural resource declining in abundance and experiencing contracting population distributions. Due to complex and extreme rocky intertidal conditions, research on growth patterns of Cellana is limited.

To reliably reconstruct Hawaiian limpet growth patterns, we applied measurements of oxygen isotopes from secondary ion mass spectrometry (SIMS) from shell line and increment features formed during growth cessation (with represented time periods in parentheses): major growth line (annual cycle), minor growth lines (lunar cycle), and minor growth increments (tidal cycle). For these culturally and commercially important mollusc shellfish, resolving growth patterns and longevity has critical implications for aquaculture, conservation, and fisheries. Here we reconstructed the life-history of the yellowfoot limpet Cellana sandwicensis from three shells, two modern and one historical, by investigating oxygen isotope variation in the tropical intertidal environment using near-daily spatial scale SIMS analysis, and (2) determining seasonal growth and longevity. This study provides a robust approach to explore tropical intertidal temperature climatology and molluscan life-history.

**Results**

Within each of the three shells of *C. sandwicensis*, five carbonate mineralogical microstructure layers were revealed by SEM and Raman microscopy in accordance with MacClintock, C. (1967). With reference to the myostracum or muscle attachment layer (M), we observed one interior layer—aragonitic, radial crossed-lamella layer (M−1)—and two exterior layers—aragonitic, concentric crossed-lamellar layer (M + 1) and calcite, concentric crossed-foliated layer (M + 2), the latter being suitable for isotope measurements (Fig. 1). The carbonate polymorph was unidentifiable for the shell’s outermost layer—a radial crossed-foliated layer (M + 3).

The observed VPDB corrected $\delta^{18}O_{calcite}$ values from SIMS of three shells ranged from $\sim-5.04\%$ to $\sim-7.74\%$ (modern specimen CW1), $\sim-4.38\%$ to $\sim-7.83\%$ (modern specimen CW2), and $\sim-5.67\%$ to $\sim-5.02\%$ (historical specimen BPBM) (see Fig. 2, Supplementary Fig. 5, Supplementary Table 1, Supplementary Table 2). Across four annual isotope cycles, the BPBM oxygen isotope profile follows a sinusoidal pattern indicative of seasonal changes in the shell records of *C. sandwicensis*. Based on analytical precision (2 standard deviations) and measurement precision.

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**Fig. 1 Shell specimens and microstructures.** Shells were sectioned from anterior to posterior end. (a) White lines represent parallel cuts for thick-section preparation from historical specimen BPBM 250851-200492. (b) Cross-sections show the true direction of growth for limpets. (c) SEM exposed shell microstructures for area denoted in b. Oxygen isotope measurements were performed along the direction of growth in the crossed-foliated, calcite layer M + 2.
(2 standard errors), the maximum uncertainty for $\delta^{18}O_{\text{calcite}}$ was 0.51‰.

The correlation between measured and calculated $\delta^{18}O_{\text{calcite}}$ were strong and significant for both modern specimens ($R^2 = 0.71$; $p < 0.0001$ and $R^2 = 0.69$; $p < 0.0001$ for CW1 and CW2, respectively) (Fig. 3). In the linear regression model, slopes were 0.39 and 0.37 for CW1 and CW2, respectively. The variance in $\delta^{18}O_{\text{calcite}}$ is likely a combined signal of $\delta^{18}O_{\text{seawater}}$ and SST.

We modeled reconstructed SST profiles for the historical shell across a range of ecologically relevant salinity values and found an effect of evaporation on $\delta^{18}O_{\text{calcite}}$ (Fig. 4). The reconstructed SST values changed by 0.84 ± 0.04 °C psu$^{-1}$. Temperature thresholds ($T_{\text{min}}$ and $T_{\text{max}}$) were most biologically relevant at salinity of 42 psu (see Supplementary Methods, and Supplementary Figure 3). At 42 psu, SST ranged from 15.5 °C to 38.0 °C and averaged 27.1 ± 7.38 °C.

The shell growth lines varied in physical appearance, which were correlated with environmental changes in the SST of the Hawaiian rocky intertidal (Fig. 5). Minor line appearance and periodicity was variable, and likely influenced by wave exposure (thick line). Micro lines were consistent and followed daily lunar cycles. We classified micro lines into two semi-lunidian increments (solid and dashed lines). During full and new moon phases, spring tides were recorded as prominent, narrow daily micro lines. During first and last quarter moon phases, neap tides were recorded as faint, wide micro lines. The major-growth lines (annual) always corresponded to the most positive $\delta^{18}O$ measurements or lowest temperature record (Fig. 2). A major-growth line was also present in specimen BPBM—in alignment with the most negative $\delta^{18}O$ measurement. However, this major band was only observed once throughout the multi-annual shell record and void in specimens CW1 and CW2. These major-growth lines were pronounced and spanned the width of M+2 layer, usually intersecting visible notches on the external surface of the shell. Minor-growth lines were observed in varying intervals of micro-growth increments (circalunidian); and micro-growth increments were subdivided by observed micro-growth lines (circalunidian). The micro-growth increment widths ranged from 6.32 μm to 61.74 μm, but were typically less pronounced and wider for neap tides in comparison to spring tides, which were very pronounced and narrow. The average micro-growth increment widths for each specimen were 22.54 μm (CW1), 20.67 μm (CW2), and 13.69 μm (BPBM). The estimated age for modern and historical specimens was 2 years (CW1 and CW2) and 5 years (BPBM), respectively. These age estimates were based on the number of annual isotope cycles, and early ontogenetic growth recorded in the apex region (beyond the last isotope measurement).

The back-calculated shell length measurements from calendar year 2017 were used to interpret sub-monthly growth rates of C. sandwicensis for the two modern specimens (see supplementary Table 4). Initial SL during this period were 20.75 mm (CW1) and 22.89 mm (CW2), respectively. Daily growth rates (DGSL) ranged from −83 μm to 588 μm, and averaged 140 ± 93 μm (CW1) and 98 ± 95 μm (CW2), respectively. Across monthly observations, DGSL was found to be highest in May for CW1 and January for CW2, respectively; and across seasons, DGSL was highest in Spring for CW1 and Winter for CW2, respectively. Total monthly growth ranged from 0 mm to 5.39 mm and were significantly correlated with both growth frequency ($R^2 = 0.81$; $p < 0.0001$; CW1 and $R^2 = 0.67$; $p = 0.0005$; CW2) and DGSL ($R^2 = 0.61$; $p = 0.0017$; CW1 and $R^2 = 0.88$; $p < 0.0001$; CW2), respectively. The total growth across calendar year 2017 for CW1 and CW2 was 19.96 mm and 15.01 mm, respectively. Modern limpets exhibited zero growth in both December and March, which lies in
the primary spawning period. These limpets also exhibited zero growth during Summer (June-July for CW2 and August for CW1), which lies in the secondary spawning period. Furthermore, interrupted growth coincided with the most extreme oxygen isotope measurements.

For the historical specimen, the annual growth rate steadily decreased from 23.22 mm in the first year to 4.50 mm in the last year and averaged 13.83 ± 7.77 mm across a total of five isotope cycles. The average daily growth rate for BPBM was 81.78 ± 120.55 µm (see Supplementary Table 3); and the maximum daily growth recorded was 605 µm. Monthly growth rates were not determined.

To compare shell growth rates, we modeled each of the three shells using a von-Bertalanffy growth function (VBGF). For the best fit VBGF model to pooled data from all three shells, parameter estimates were $L = 75.233$ (±2.681 SE) and $K = 0.0371$ (±0.0021 SE) with $t_0$ constrained to represent an initial length of post-larval settlement of 0.254 mm observed for C. sandwicensis (Fig. 6);29–31. Modeled shell length at one year is 27.2 mm, two years is 44.5 mm, three years is 55.5 mm, four years is 62.6 mm, and five years is 67.1 mm. No differences in growth model parameter estimates between pairwise comparisons of individual shells were found for all $\chi^2$ statistics ($p > 0.05$) from likelihood ratio tests.

Discussion
We used secondary ion mass spectrometry (SIMS) analysis to achieve sub-weekly to daily spatial scale resolution in the oxygen isotope profile of a tropical rocky intertidal marine mollusc (Cellana sandwicensis). Isotope measurements were extracted from an area of 15 µm² across the shell growth axis, which accounts for one to three growth days of any shell. To the best of our knowledge, this methodology represents the highest attainable spatio-temporal resolution for paleoecology of a tropical intertidal limpet.

The linear relationship between calculated and measured $\delta^{18}$O validates the use of molluscan shell records for seasonal interpretations of growth and life-history. At this time, however, we cannot conclude biogenic calcite to be in equilibrium with seawater. Future studies should focus on validating this mollusc limpet as a proxy for sea surface temperature by comparing $\delta^{18}$Ocalcite and $\delta^{18}$Oseawater using both conventional gas source mass spectrometry (GSMS) and SIMS analytical methodologies. This would contribute to the ongoing work to refine the interpretation of $\delta^{18}$O measured by SIMS in biogenic carbonate.

There was a seasonal shift in the relationship between calculated and measured $\delta^{18}$O for modern specimens. We do not, however, totally discount the possibility that modifications in seawater chemistry of the extrapolial fluid are influencing...
calcification in *C. sandwicensis* (Langer et al. 2018); and vital effects (i.e., physiology, metabolism) are known to interfere with oxygen isotope fractionation that cause discrepancies in molluscan climate proxies.

To calculate oxygen isotope equilibrium fractionation (Eq. 1), we chose to apply an average salinity value for the study site; and because SSS and δ^{18}O_{seawater} are highly correlated, our resulting changes in δ^{18}O_{calcite} are driven by seasonal temperature fluctuations.

Given δ^{18}O_{seawater} was not measured directly, our maximum uncertainty of 0.51‰ may be slightly underestimated as surface δ^{18}O_{seawater} is somewhat influenced by wet and dry seasons. We did not observe any major anomalies in the shell records. Rainfall events were previously thought to challenge interpretation of oxygen isotope profiles in tropical environments. We suggest that precipitation at both the modern shell (Ka’alawai) and the historical (unknown) sites occurs infrequently and the distance between isotope measurement locations were too far to detect these alterations in carbonate chemistry. Moreover, aside from rainfall and groundwater discharge, microhabitats within the same littoral zone vary tremendously with respect to evaporation, and are perhaps contributing to intraspecies variation in carbonate chemistry. For instance, limpets inhabiting aerially exposed rock features may result in a wider δ^{18}O_{calcite} range than subsurface limpets.

We reconstructed the past marine environment for an archival specimen (BMBP) by modeling proxy temperature regimes across a range of predicted salinities. We observe proxy temperature to approach a biologically relevant range at 42 psu. Given that our archival shell was recently collected (not part of a midden), the isotopic results suggest that both the δ^{18}O and SSS in the Hawaiian intertidal were possibly elevated by evaporation. At a salinity of 42 psu, we interpret this historical specimen’s environment to be more aerially exposed compared to that of modern specimens, where extreme upper- and lower-threshold temperatures are likely a result of solar irradiance and evaporative cooling, respectively.

To address the precision of our inferences, we must consider that variability in the δ^{18}O_{seawater}—SSS relationship may introduce error up to 1.5 PSU in the Tropical Pacific. Fortunately, when considering this relationship in the recent geologic time scale, there has been only marginal fluctuations. Henceforth, our current methodology should also support sound palaeoecology research using tropical archeological middens dating as far back as early Polynesian settlement (AD 800) in the Hawaiian Islands. We discuss in further detail the thermal thresholds to growth, patterns in shell growth, and longevity of *C. sandwicensis* interpreted from the study.

**Thermal threshold.** The observed seasonal minimum and maximum δ^{18}O_{calcite} vary by shell record, and thresholds appear to change across time and space. Historical specimen BMBP recorded the widest δ^{18}O range, and according to the model, did not grow below 15.5°C or above 38.0°C. Based on Hawaiian rocky intertidal substratum temperatures (15°C to 40°C), we understand this to reflect true thermal range for yellowfoot limpet. Comparatively, modern specimens from Ka’alawai recorded a less extreme range of δ^{18}O values, which may suggest differences between the individuals’ positioning within the intertidal environment.

**Growth patterns.** Tropical limpets are exposed to mixed, semi-diurnal tides, which plays a role in growth line formation. Tide patterns allowed us to temporally align growth features around anchors (δ^{18}O min/max) similar to previous studies on temperate limpet species. These patterns, however, were often interrupted at random causing inconsistent daily band widths. We attribute these inconsistencies to be influenced by waves, which dominate Hawaiian rocky intertidal shorelines.

Besides tidally influenced growth patterns, modern specimens exhibited a decrease in daily growth rate prior to complete stoppage in somatic growth in primary and secondary spawn periods, respectively. Although associated with spawning activity, it also appears that seasonal changes in growth rate are attributed to their response to desiccative conditions and temperature extremes.

In a controlled study by Mau and Jha, feeding, growth performance and mortality of *C. sandwicensis* were negatively affected by mean air temperatures >28.5°C. These captive limpets also exhibited similar seasonal trends observed in CW2—growth rates were lowest in Fall and highest in Winter—and further indicates that growth follows changes in climate.

All limpets in the current study exhibited determinate growth (Fig. 6), where predictable changes in daily growth rate occur during ontogenetic shift from juvenile to adulthood (See
Supplementary Table 3). This type of growth, exhibited by yellowfoot limpet, is common in Tropical Pacific gastropods38. Age-at-maturity is an important metric for understanding population dynamics and assessment of managed stocks. For our isotopically analyzed yellowfoot limpet, age-at-maturity was 8–9 months (~21 mm shell length) which differed from a prior report of 4–7 months (Kay et al., 1981). The discrepancy between current and previous reports most likely arose because the previous authors assumed limpets <5 mm to be 1 month in age. There was intra-species seasonal variability in growth, where highest mean daily growth rates were observed in May (CW1) and January (CW2), respectively. Frequency of growth, however, was consistently highest in Fall, which precedes the primary spawning window. Based on timing of maximal somatic growth and GSI, we understand that C. sandwicensis is likely bulking for reproduction twice, annually (see Supplementary Equation 1 and Supplementary Fig. 1).

Monthly growth rates changed with frequency of growth days, and consistent growth cessation periods aligned with previously described spawning periods in both Winter and Summer months (longest period of missing growth was ~3 months). The differences in seasonal growth patterns between individuals from the same population likely result from genetic variability (circadian rhythm) and environment (food availability and micro-habitat).

Longevity. Our sclerochronology of temporally aligned shell records provides the first reliable age estimate of C. sandwicensis. The historical specimen represents the maximal size (68.6 mm SL), and indicates this species to live up to 5 years. The longevity of C. sandwicensis is similar to that reported for related species: C. tramoserica (3yrs), C. radiata (4yrs), C. eucosmia (5yrs), and C. karachiensis (6yrs), which indicates that Cellana is a relatively short-lived clade39–42. In theory, the longevity of marine gastropods is selected by environmental and biological pressures to ensure reproductive success43. For C. sandwicensis, longevity may be influenced by wave exposure, average limpet size, population density, substratum type, and human harvesting. Current, ongoing research is focusing on these variables to evaluate their impact to the Hawaiian limpet fishery, and to establish adaptive management strategies.

Methods

Ecology of Yellowfoot limpet. In the Tropical Pacific, sympatric limpets (Cellana melanostoma, Cellana exarata, Cellana sandwicensis, Cellana talcosa) inhabit the Hawaiian rocky intertidal ecosystem, where they graze on crustose coralline algae (CCA) and epibenthic microorganisms. Distribution ranges from the splash zone (upper-intertidal) to subtidal zone, and across the entire Hawaiian Archipelago44. They are dispersed across the majority of seamounts, atolls, and islands, however, not all species are present in every rocky intertidal locality, which reflects species-specific disturbances and habitat preferences. The reproduction cycles for each species appears to vary in time and space, and on-going long-term monitoring efforts are in progress to define this critical life-history trait. Previous studies on the yellowfoot limpet C. sandwicensis, reveal that reproduction is highly synchronized from December to March27,29. Gametogenesis also occurs from June to August, however, the level synchronicity and intensity of this second spawn period are inconsistent. These limpets are gonochoristic and considered to be sequential hermaphrodites43. The sex ratio is near 1:1(M:F) during spawning season, however, also occurs from June to August, and reduces likelihood of hybridization between sympatric species.

Modern and historical specimens. On June 28th of 2018, live Yellowfoot limpet (Cellana sandwicensis) specimens CW1 and CW2 were collected from the rocky intertidal zone at Ka’alawai, Oahu, Hawai‘i (Fig. 7). The animals were immediately sacrificed dissected using scalpel blade, and measured for shell dimensions using a caliper. Limpets were weighed to determine gonadosomatic index, and gonads were preserved for histological examination. Shells were rinsed in an ultrasonic bath and air-dried. A historical specimen BPBM (identification number 250851-200492) was loaned from the Bernice Pauahi Bishop Museum Malacology Department Collection. This specimen’s geographical and ecological origin is unknown, but was identified as C. sandwicensis by its characteristic shell morphology45. This specimen was selected for its large size to estimate life-expectancy of this limpet species, as well as to evaluate this method for paleoecological studies. Permission was not required to obtain specimens used in this study, and limpets were collected at a size exceeds the legal minimum shell length of 31.8 mm (Hawaii State Law is enforced by Department of Land and Natural Resources). Ethical approval was not required for conduct analysis.

Characterization of shell microstructure. Shell microstructure was identified before isotopic analysis could be attempted. Each shell was cross-sectioned from anterior to posterior direction using a low speed saw (Isomet 1000, Buehler) equipped with a 0.5 mm diamond coated blade. Parallel cuts were made at the apex or maximum growth-axis to obtain two replicate 1.3 mm thick-sections per specimen. The first replicate thick-sections, prepared for micro-sampling, were further cut into <15 mm long pieces and mounted on a single glass round, and the second replicate thick-sections, prepared for sclerochronology, were mounted in its entirety on a large glass slide. Specimens were mounted in using quick-drying epoxy (EPO-TEK 301, Epoxy Technology Inc, Billerica, MA) set in a mold, ground with F1000 grit SiC powder, secosecondary, and polished with 3 µm and 1 µm Al2O3 powder on a lapping wheel. Polished sections on glass rounds were then sonicated, rinsed with methanol, and carbon-coated to ~250 Å (Cressington Carbon Coater 208carbon, Watford UK). Microstructures of unstained specimens were identified by Scanning Electron Microscopy (SEM); JEOL JSM-5900LV, USA) photography following MacCluskey and Rampleman46. Raman spectroscopy was used to characterize biogenic carbonate mineralogy by comparing shifts in relative peak position and intensity between calcite and aragonite polymorphs47 (see Supplementary Fig. 4). A silicon wafer standard was used to determine spectral center w of TiO2 was 800 gosangs/nm. Single spectrum analysis was performed in each microstructure layer using a green laser at 514 nm. A total of six (n = 6) sampling sites were selected haphazardly for a given microstructure layer, which comprised of ten accumulations averaged across 10,000 s. The shell’s exterior surface layer did not return clear spectral peaks, and thus has been excluded from our analysis.

Secondary ion mass spectrometry analysis. Hawaiian limpet Cellana sandwicensis shells CW1, CW2, and BPBM were analyzed for oxygen isotopes. Polished thick-sections were imaged by light and scanning electron microscopy (SEM) to guide sampling by ion microprobe. We sampled in the cross-foliated, calcite
The growth axis. Measurements were performed moving from the shell margin toward the apex along the growth axis.

To achieve sub-weekly resolution for an annual δ¹⁸O cycle, modern specimens, CW1 and CW2, were analyzed using an average interval of 252 µm and 288 µm between samples, respectively. To achieve sub-annual resolution across multiple δ¹⁸O cycles, the historical specimen, BPBM 250851-200492, was analyzed using an average interval of 554 µm. The total number of microprobe sample measurements was 55, 43, and 36 for CW1, CW2, and BPBM, respectively. A single, annual isotope cycle was analyzed for the modern specimens, and four annual isotope cycles were analyzed for the historical specimen.

The reproducibility measurements (2σ) of UWC-3 reference material ranged from ±0.17 to ±0.35‰, which reected measurement precision and reproducibility of δ¹⁸Ocalcite. Following SEM and SIMS, we removed the carbon-coated thick-sections were placed under vacuum conditions to prevent contamination prior to being measured by CAMECA-IMS-1280 ion microprobe (SIMS; W.M. Keck Research Laboratory, University of Hawai‘i) for oxygen isotopes. The primary ion beam C⁺ was set at 2.5 nA for 120 s presputtering. Ions were extracted at ~8 kV. Microprobe rastered across a 15 µm² area, which accounted for 1-3 lunar daily growth increments. Each measurement included 30 cycles with 10 s integration period. The ¹⁸O and ¹⁶O were measured in multicollection mode using two Faraday cups with 10¹⁰ and 10¹¹ Ω registers, respectively. The b-field was controlled by nuclear magnetic resonance. Mass resolving power was 1958 % min⁻¹, which allows detection of possible interference ions. To correct for instrumental isotope mass fractionation, University of Wisconsin Calcite, UWC-3 (δ¹⁸O = 12.49‰ Vienna Standard Mean Ocean Water – VSMOW), was measured consecutively before and after performing microprobe analyses for each specimen (n = 12)⁵². Corrections were made based on these groups of standard measurements with limited monitoring for instrumental drift. The reproducibility measurements (2σ) of UWC-3 reference material ranged from 0.17 to 0.35‰, which reflected measurement precision and reproducibility of standard measurements for same-day measurements. Measurement errors are reported as 2σ, which reflects both precision (2 standard error) and reproducibility (2 standard deviation) (see Supplementary Data 1 and Supplementary Data 2). Following the microprobe analyses, shell samples were imaged under SEM to expose sample scars for sclerochronology.

Predicted shell δ¹⁸O. To examine if Hawaiian limpet shells are in isotopic equilibrium with their environment, we compared measured δ¹⁸Ocalcite to predicted δ¹⁸Owater calculated from seawater-surface temperatures (SST) and surface seawater salinity (SSS). Sea-surface temperatures were obtained from in-situ PacIOOS Nearshore Sensor 04 (NS04) at the Waikiki Aquarium.

Anchoring points. Calendar dates (based on a lunar year) were assigned for every isotope measurement between these anchors by counting micro lines (lunar daily growth). We applied previous research on growth and reproduction to resolve alignment discrepancies between predicted δ¹⁸Ocalcite and measured δ¹⁸Ocalcite.
Climate reconstruction of historical shell. The exact location from which the historical specimen SMBP was collected is unknown. Climate was reconstructed from the shell isotope record—assuming that δ18Ocalcite is precipitated in equilibrium with δ18Owater. Sea surface temperature was calculated from sequentially sampled isotope measurements across ecologically relevant salinity values. Based on the profile with the most biologically relevant temperature thresholds (min and max), we predicted historical sea surface salinity (SSS).

Growth measurements. The polished over-sized, thick-sections were stained with Mutvet’s solution to expose major lines, micro lines, and minor increments by light microscopy. Shell-thick-sections were placed in a petri dish and submerged in Mutvet’s solution for 45 min held constant at 37–40 °C with constant stirring. These stained thick-sections were imaged using Nikon Eclipse E600 Polarisizing light microscope at 100x magnification for performing growth line measurements.

Daily growth was measured along two axes using the standard measuring tool in ImageJ. The first type of daily growth was measured between two micro increments along the growth axis. The second type of daily growth was measured along the horizontal axis (anterior to posterior orientation).

For each lateral recorded x-coordinates for each point where a micro increment band intersected the M + 3 layer, and subtracted x-coordinates of sequential points to calculate horizontal distance or growth. Back-calculated shell lengths were used to model age-at-length data (see Supplementary Eq. 2, Supplementary Fig. 2).

We analyzed sub-monthly growth of modern specimens across an annual isotope cycle to understand temporal changes in growth. This period was selected based on the shell length at which C. sandwicensis enters adulthood, which allows interpretation of adult growth (Kay et al. 1983).

Shell growth model. We used the back-calculated measurements of shell length-at-age as data inputs to estimate parameters of the von Bertalanffy growth function (VBGF) (Eq. 5), a standard method of describing growth in marine animals. The VBGF (Eq. 5) was fit to shell length (in mm) at age (in months) data for each shell individually (i.e., CW1, CW2, BH) and pooled samples using non-linear parameter estimation:

\[ L(t) = L_{\infty} \left(1 - e^{-Kt(t-t_0)}\right) \]

where \( L(t) \) is length (mm) at age \( t \) years, \( L_{\infty} \) is the mean asymptotic length (mm), \( K \) is the growth coefficient, and \( t_0 \) is the theoretical age at length zero. Growth curves were fit by constraining \( L_{\infty} \) to a common shell length of settlement in order to increase the accuracy of VBGF parameter estimates. The length at post-larval settlement (i.e., \( L_S \)) of Cellana sandwicensis was obtained from existing literature as 0.234 mm ± 0.0038 mm. To determine if measurements from all shells could be pooled for a single growth model, we used likelihood ratio tests to test for pairwise differences in \( L_S \) and \( K \) between shells by generating a \( \chi^2 \) statistic for each set of comparisons (sensu 55, 56, Haddin, 2011). Growth data for the pairwise comparisons were truncated to a shell length range of 0–45 mm that represented the range of data overlap for all three shells to minimize bias from the larger maximum size of shell RPMs. We used R v3.3.1 (R Core Team, Vienna, Austria), and Excel 2013 (Microsoft Corporation, Redmond, WA, USA) to perform the growth model statistical analyses.

Statistical analysis. Unless stated otherwise, all statistical analyses were accomplished in SAS (SAS v9.2, SAS Institute Inc., Cary, NC, USA). Pearson’s correlation coefficients were computed using Proc CORR to determine linear relationships between SSTcalculated and SSTmeasured. We also used correlation analysis to describe VBGF, a standard method of describing growth in marine animals. The at-age as data inputs to estimate parameters of the von Bertalanffy growth function allows interpretation of adult growth (Kay et al. 1983).

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability. Data can be found in a publicly accessible repository. The raw and processed temperature data for this study is available at https://doi.org/10.6084/m9.figshare.15050274. The raw and processed isotope measurement data for modern and historical shells are available at https://doi.org/10.6084/m9.figshare.15050256. The Bertalanffy growth model for Hawaiian limpet Cellana sandwicensis is available at https://doi.org/10.6084/ m9.figshare.15050238. The raw and processed oxygen SIMS-derived oxygen isotope data for modern and historical specimens are available at https://doi.org/10.6084/ m9.figshare.15050235.

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Data can be found in a publicly accessible repository. The raw and processed temperature data for this study is available at https://doi.org/10.6084/m9.figshare.15050274. The raw and processed isotope measurement data for modern and historical shells are available at https://doi.org/10.6084/m9.figshare.15050256. The Bertalanffy growth model for Hawaiian limpet Cellana sandwicensis is available at https://doi.org/10.6084/ m9.figshare.15050238. The raw and processed oxygen SIMS-derived oxygen isotope data for modern and historical specimens are available at https://doi.org/10.6084/ m9.figshare.15050235.
