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Biogeography of shell morphology in over-exploited shellfish reveals adaptive tradeoffs on human-inhabited islands and incipient selectively driven lineage bifurcation

Adaptive tradeoffs in shell morphology

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68

69 **ABSTRACT**

70 **Aim:** To identify potentially human-mediated biogeographic patterns in selection and adaptive
71 tradeoffs affecting the evolution an over-exploited shellfish.

72 **Location:** Hawaiian Archipelago

73 **Taxon:** Mollusca, Gastropoda, Patellagastropoda, Nacellidae, *Cellana exarata*, ‘Opihi makaiauli

74 **Methods:** We surveyed phenotypic characters associated with temperature and predation
75 avoidance across the entire species range and tested for differences in the relationship between
76 these characters and latitude, on islands with and without humans.

77 **Results:** Among all limpets surveyed, there was a bimodal distribution in shell color (light, dark)
78 and a parapatric pattern of shell coloration across the archipelago with lighter shells being
79 prevalent on the uninhabited islands and darker, more camouflaged shells being prevalent on the
80 inhabited islands. On the cooler, uninhabited islands, all morphometric characters associated
81 with thermal avoidance (surface area, height, and doming) increased with decreasing latitude. On
82 the hotter, inhabited islands, however, shells were flatter, less variable, and less adapted for
83 avoiding thermal stress than predation.

84 **Main Conclusions:** The biogeographic patterns in shell phenotype and previous genetic studies
85 suggest that the population is beginning to bifurcate in response to disruptive and directional
86 selection as well as geographic isolation between the islands with and without humans.

87 Decreased phenotypic and genetic diversity on the inhabited islands despite much larger
88 populations of ‘opihi suggests a prominent historical bottleneck. The prevalence of maladaptive
89 dark, flat phenotypes for thermal avoidance on the inhabited islands suggests that predation is a
90 stronger selective force, driving adaptive tradeoffs in shape and color. We propose that this is
91 likely a case of fisheries-induced evolution and a millennium of harvesting is the most likely

92 selective pressure driving the observed biogeographic patterns in shell morphology. The flatter,
93 darker shells will allow body temperatures to rise higher in direct sunlight, therefore we
94 hypothesize that the thermal niche of ‘opihi is narrower on inhabited islands and will continue to
95 narrow as Earth warms. This study highlights the utility of using intraspecific biogeographic
96 patterns in phenotype to identify adaptive tradeoffs in response to varying selective pressures and
97 identify nascent ecologically driven lineage splitting.

98

99 **Keywords:** fisheries-induced evolution, adaptation, adaptive capacity, climate change resilience,
100 phenotypic variation, morphometrics

101

102

103 1 INTRODUCTION

104

105 Variation in the selective landscape can drive the phenotypic structure in populations
106 (Johnson & Barton, 2005); therefore, biogeographical patterns of phenotype can be indicative of
107 variation in underlying selective pressures (Mayr, 1963). Selection acts on phenotypes;
108 consequently, acclimation and adaptation to selective pressures present as changes in the
109 frequency distribution of phenotypes (Belonsky & Kennedy, 1988; Lande & Arnold, 1983).
110 Selective pressures can drive local adaptation (Blondel, 2008; Guo, DeFaveri, Sotelo, Nair, &
111 Merilä, 2015; Lind, Ingvarsson, Johansson, Hall, & Johansson, 2011), population structuring
112 (Bekkevold et al., 2005; DeFaveri, Jonsson, & Merilä, 2013; Schemske, 1984), and even lineage
113 diversification (Pavlova et al., 2013; Shepard & Burbrink, 2011), especially when correlated with
114 gene flow restrictions (Blondel, 2008; Lind et al., 2011; Schemske, 1984). Selection can also
115 affect phenotypic diversity, with both directional and stabilizing selection reducing phenotypic
116 variation (Hoekstra et al., 2001; Lemos, Meiklejohn, Cáceres, & Hartl, 2005). On the other hand,
117 disruptive and balancing selection maintain phenotypic diversity, and spatio-temporal
118 heterogeneity in selective forces can promote increased phenotypic variation (Rainey &
119 Travisano, 1998).

120 The extent of phenotypic variation and limits on the adaptation of any single phenotype
121 are governed by the effects of adaptive tradeoffs on the overall fitness of an organism (reviewed
122 in Agrawal, Conner, & Rasmann, 2010). A single-trait tradeoff occurs when multiple selective

123 pressures affect a single phenotype, preventing the maximization of fitness in response to any
124 one of the multiple selective pressures. Single-trait tradeoffs can lead to polymorphisms when
125 selective pressures vary in space due to either local adaptation or phenotypic plasticity (Agrawal
126 et al., 2010; Futuyma, 2013). For example, the shell thickness of the intertidal snail *Littorina*
127 *obtusata* covaries with predation pressure at the expense of body mass and, presumably,
128 physiological maintenance of the organism (Trussell, 2000).

129 Adaptive tradeoffs and selective landscapes can be influenced by anthropogenic
130 activities, leading to human-induced evolution (Hendry, Gotanda, & Svensson, 2017). For
131 example, anthropogenic activities have indirectly led to a tradeoff in offspring quantity and
132 quality in peacock butterflies (*Aglais io*) where there is increased offspring survival in less
133 impacted landscapes but increased fitness in the few offspring produced in more impacted
134 landscapes (Serruys & Van Dyck, 2014). The direct selective pressures that lead to fisheries- and
135 harvest-induced evolution can have even stronger effects (Heino, Pauli, & Dieckmann, 2015;
136 Kuparinen & Fests-Bianchet, 2017).

137 Two strong selective pressures that are influenced by humans and vary across
138 biogeographic space are temperature and predation. (1) Temperatures generally increase with
139 decreasing latitudes, increased exposure to solar irradiance, and can drive adaptations to tolerate
140 or avoid stressful conditions, especially in ectotherms (Veryheyen & Stoks, 2018). Temperatures
141 are also increasing in conjunction with rising levels atmospheric carbon dioxide (Snyder 2016),
142 pushing ectotherms closer to their thermal limits (Pinsky, Eikeset, McCauley, Payne & Sunday,
143 2019). Adaptations in ectotherms enabling thermal regulation and avoidance can be effective in
144 ameliorating thermal stress. For example, ectotherms can seek thermal refuges (Dillon, Liu,
145 Wang, & Huey, 2012) or employ behaviors that modulate temperature (Miller & Denny, 2011;
146 Seuront & Ng, 2016). Morphological features, such as shell size and shape in gastropod snails,
147 can affect the body's heat budget (Denny & Harley, 2006; Harley, Denny, Mach, & Miller
148 2009), and lighter coloration can decrease the absorbance of solar irradiation which can result in
149 decreased body temperature (Geen & Johnston, 2014; Pereboom & Biesmejer 2003; Trullas, van
150 Wyk, & Spotila, 2007). (2) Predation is often correlated with other habitat and environmental
151 characteristics (Beukers & Jones, 1998), and in edible species, proximity to humans can be an
152 important predictor (Cinner, Graham, Huchery, & MacNeil, 2013; Williams et al., 2008).
153 Adaptations in response to predation include a decrease in mean body size (Meiri, 2008; Ratner

154 & Lande, 2001; Trussell, 2000), increased frequency of protective characters (Caley & Schuler,
155 2003; Leonard, Bertness, & Yund, 1999; Trussell, 2000), and cryptic coloration (Merilaita et al.,
156 2001, Miller & Denny, 2011). For example, mussels have been shown to exhibit an increase in
157 shell strength and more tightly attach to substrate due to predation (Leonard et al., 1999).

158 In intertidal ectotherms, such as patellogastropods, both predation and thermal stress can
159 be intense (Branch, Trueman, & Clark, 1985; Knight, 2011; Lowell, 1984; Vermeij, 1973).
160 Under thermally stressful conditions which occur during periods of emersion and direct solar
161 irradiance in the middle of the day, lighter-colored, taller shells with greater surface area are
162 advantageous in limiting thermal and desiccation stresses (inferred from Denny & Harley, 2006).
163 Lighter colors reflect solar irradiation (Miller & Denny, 2011); shells with greater surface area
164 can shed more heat to the atmosphere (Denny & Harley, 2006); and taller shells can experience
165 greater wind velocities, aiding in heat dissipation (Harley et al., 2009), while absorbing the same
166 amount of solar irradiation as shorter shells with less surface area (calculated from Pennell &
167 Deignan, 1989, see Denny & Harley, 2006). Indeed, a pattern of increasing shell height with
168 decreasing latitude was observed in the limpet, *Patella depressa*, on the Iberian peninsula (Hines
169 et al., 2017).

170 Flatter, cryptically colored shells, however, are advantageous in avoiding predation,
171 setting up a potential tradeoff with morphologies that ameliorate thermal stress (Hines et al.,
172 2017). Predators such as fishes and crabs cannot prey as efficiently on flatter-shelled limpets
173 because both crushing the shell apex (Lowell, 1986; Vermeij, 1993) and applying lateral force
174 for dislodgement is more difficult. Cryptically-colored shells that blend into the background are
175 also more difficult for predators to detect (Miller & Denny, 2011) and is an important
176 mechanism of survival for intertidal gastropods (Manríquez, Lagos, Jara, & Castilla, 2009).
177 Sorenson and Lindberg (1991) concluded that *Lottia pelta* limpets with less cryptic shell
178 coloration were more commonly consumed by American black oyster catchers (*Haematopus*
179 *bachmani*), and Mercurio, Palmer, and Lowell (1985) employed experimental transplants to
180 demonstrated that cryptic coloration results in lower rates of predation in the limpet, *Collisella*
181 *digitalis*, by both fishes and birds.

182 The over-exploited, endemic Hawaiian limpets, *Cellana spp.*, provide an ideal
183 opportunity to test for adaptive tradeoffs in shell morphology where thermal stress and predation
184 are negatively correlated. *Cellana exarata*, locally known as ‘opihi makaiauli, are high-intertidal,

185 endemic, monocious broadcast-spawners with a 2-14 day pelagic larval duration. *Cellana*
186 *exarata* ranges along a latitudinal and thermal gradient from ‘Ōnū (Gardner Pinnacles, 25°N) to
187 the Big Island of Hawai‘i (19°N) where the morphology transitions from light-colored and tall-
188 shelled to dark-colored and flat-shelled (Kay & Shoenberg-Dole, 1991). All of the islands are
189 predominantly composed of dark basaltic substratum, which makes lighter, solar irradiance-
190 reflecting shell colors disadvantageous in the face of predation pressure, while darker shells are
191 more camouflaged from predators. In the hotter Main Hawaiian Islands (MHI, Kaua‘i –
192 Hawai‘i), ‘opihi have been intensely harvested (Kay & Magruder, 1977; McCoy, 2008) ever
193 since they were colonized, A.D. 940-1130 (Athens, Rieth, & Dye, 2014). The uninhabited,
194 cooler Northwestern Hawaiian Islands (NWHI) are subject to lower predation pressure since all
195 but one of these islands (Nihoa) have never been settled by humans (Kikiloi et al., 2017) and
196 they are presently within the Papahānaumokuākea Marine National Monument where harvest by
197 humans is largely illegal. Further, the NWHI harboring ‘opihi are small (<69 hectares) and
198 devoid of terrestrial predators capable of consuming adult ‘opihi such as rats and mongooses.

199 The Hawaiian archipelago provides ample opportunity for physical and genetic isolation
200 among islands (Toonen et al., 2011), which can foster local adaptation (Blondel, 2008). Indeed,
201 there are gene flow restrictions in *C. exarata* among islands with varying levels of genetic
202 isolation across the archipelago (Bird, Holland, Bowen, & Toonen, 2007; Cockett, 2015).
203 Importantly, the most pronounced genetic isolation is found between the uninhabited NWHI and
204 inhabited MHI. Cockett (2015) also found that genomic diversity decreased, on average, from
205 the smaller populations in the NWHI to the larger populations in the MHI, a signature of a
206 historical population bottleneck. Despite these genetic patterns and morphological differences
207 between the NWHI and MHI ‘opihi, genetic investigations have been unable to identify species-
208 level differentiation (Samollow, pers. comm. (allozymes); Reeb, 1995 (mtDNA); Bird, Holland,
209 Bowen, & Toonen, 2011 (mtDNA & nDNA); Cockett, 2015 (RADseq)).

210 Here we conduct the first rigorous investigation of the biogeography of shell morphology
211 and coloration in *C. exarata* across the entire species range. We test for a decline in
212 morphometric variation from the NWHI to the MHI that parallels the genetic pattern reported by
213 Cockett (2015). We hypothesized that if thermal and desiccation stress were the dominant
214 selective pressures affecting *C. exarata*, then shells would be progressively lighter-colored and
215 taller with greater surface area down the latitudinal gradient. We test this hypothesis on both the

216 inhabited and uninhabited islands to test for a competing effect of predation on the adaptation of
217 ‘opihi to thermal stress. If predation is the most important selective pressure, then we expect that
218 shells would be flatter and darker, making the ‘opihi more difficult to detect and dislodge from
219 the substratum. We conclude by discussing the observed biogeographic patterns and the potential
220 role of humans in the evolution of ‘opihi.

221

222 **2 MATERIALS AND METHODS**

223

224 **2.1 Sample Collection and Geographic Metadata**

225 Living and presumably healthy *Cellana exarata* were collected from eight Hawaiian
226 Islands between 2012 and 2016: ‘Ōnū (ON, Gardner Pinnacles, Puha honu), Lalo (LA, La
227 Perouse Pinnacles, Mokupāpapa), Mokumanamana (MM, Necker), Nihoa (NI), Kaua‘i (KA),
228 O‘ahu (OA), Maui (MA), and Hawai‘i (HI, Big Island; Table 1; Kikiloi et al., 2017). The NWHI
229 were accessed during intertidal monitoring cruises sponsored by Papahānaumokuākea Marine
230 National Monument, and eight ‘opihi were collected from each of six, 1 cm size classes. In the
231 MHI, shells of legal harvesting size (> 3 cm) were haphazardly collected along a 7 km section of
232 coastline on Maui, two locations on Kaua‘i (Miloli‘i and Kekaha) and O‘ahu (Kaka‘ako, ‘Āina
233 Moana), and one location on each of the remaining islands. All sites were composed of natural
234 basalt formations with the exceptions of the O‘ahu and Hawai‘i sites (basalt riprap) and Kekaha
235 (emergent coral reef). Site selection was largely haphazard because shell morphology (at the
236 level investigated here) was observed to be more homogenous within than between the NWHI
237 and MHI. For example, Bird (2011) found very small differences in shell shapes among five
238 disparate locations in the MHI, four of which were on the Big Island of Hawai‘i. Kekaha, Kaua‘i,
239 however, was deliberately targeted because its light-colored, emergent coral reef substratum was
240 known to harbor a light-colored morphotype of *C. exarata*. Overall, there was no meaningful
241 confounding of human habitation, the selection of survey sites within islands, and the individuals
242 collected for analysis.

243 Geographic location information for each sampling site was obtained using Google Earth
244 Pro 7.3.2.5776. The one-dimensional geographic location of each sampling site was recorded as
245 the stepping-stone distance (Bird et al., 2007) between the Northwestern-most island harboring
246 *C. exarata*, ‘Ōnū, and the island of each sampling site. Stepping-stone distance is defined as the

247 sum of the channel widths at their narrowest between the reference island, in this case ‘Ōnū, and
248 the island of each sampling site. Stepping-stone distance was used rather than the distance
249 between sampling sites because it was the best predictor of isolation in *C. exarata* as inferred by
250 mitochondrial genetic differentiation (F_{ST}) and gene flow ($N_e m$) among population samples (Bird
251 et al., 2007). Conceptually, stepping-stone distance is an estimate of isolation that is defined as
252 the minimum distance a pelagic larva could travel between two islands, and direct exchange
253 between non-adjacent islands is assumed to be negligible (Bird et al., 2007). We acknowledge
254 that larvae will travel more circuitous routes as they disperse and may disperse to non-adjacent
255 islands, but nonetheless, stepping-stone distance is the best model of isolation for the study
256 species.

257

258 **2.2 Character State Scoring, Missing Data Imputation, and Allometric Normalization**

259 The newest parts of the shell (rib tips) were used to classify shell color based upon the
260 expression of dark periostracum, the proteinaceous shell coating, and irrespective of shell
261 erosion. Rib tip color was scored estimating the percentage of rib tips that had dark pigment in
262 increments of 25% in each of four quadrants and averaging the scores for each shell. If $\geq 50\%$
263 of rib tips were dark, the color morphotype of the shell was classified as dark-colored. Otherwise
264 the shell was classified as light-colored.

265 We were primarily interested in investigating morphometric characters related to thermal
266 avoidance: shell surface area and shell height. We measured shell height (H), length (L), and
267 width (W) directly using dial calipers and inferred surface area by modelling the shell as an
268 ellipsoid cone (Table 2). Because the lateral area of a cone does not account for shell doming, we
269 calculated a doming index based upon the lateral length from the apex to posterior margin of the
270 aperture along the axis of symmetry in the shortest distance possible ($L_{1,3}$) and along the curve of
271 shell’s surface ($C_{1,3}$, Figure 2) using ImageJ (Schneider, Rasband, & Eliceiri, 2012) and images
272 taken from the lateral perspective (see Figure 2). Landmarks defined by cartesian coordinates
273 were placed on either end of a size standard, the apex (Point 1), the anterior (Point 2) and
274 posterior aperture edge (Point 3). The lengths ($L_{1,3}$, $L_{2,3}$) were calculated using the Pythagorean
275 Theorem, while $C_{1,3}$ was determined by drawing a line using the segmented line tool from point
276 1 to 3 along each shell’s edge, and then converted to mm using the size standard. Finally, a scale

277 correction factor to align ImageJ measures with those from the calipers was determined by
278 dividing L_i by $L_{2,3i}$, where i is each individual's identity and was multiplied by $L_{1,3i}$ and $C_{1,3i}$.

279 Since some shells were missing either length or width data due to shell damage, we
280 imputed the missing data based on the present width or length respectively. The best models
281 between a linear and power function for imputing L from W and vice-versa were identified by
282 satisfying the assumptions of least-squares regression models, minimizing the Akaike
283 Information Criterion (AIC) and testing against the null model using a log-ratio test.
284 Heteroscedasticity was explicitly modeled with an exponential variance structure to make the
285 final models (Table S1, Figure S1).

286 All morphometric measurements were normalized by the mean shell length to remove the
287 effects of allometry using the following equations:

288
$$Y = aL^b \quad \text{and} \quad Y_i^* = Y_i \left[\frac{\bar{L}}{L_i} \right]^b,$$

289 where Y is the size of a character (W , H , $L_{1,3}$, $C_{1,3}$), i is an individual's identity, L is the shell
290 length, \bar{L} is the mean shell length, and a and b are constants (Lleonart, Salat, & Torres, 2000).
291 These relationships were tested as described for the imputations (Table S2). To better satisfy the
292 assumptions of each model, the L and Y were natural log-transformed except in the case of width
293 because all assumptions were met without a transformation (Figure S2). After allometric
294 normalization, all individuals smaller than 25 mm in length were excluded from the study
295 because juveniles tend to have different morphologies from adults due to ontological changes
296 (Vermeij, 1973). From the allometrically-normalized measurements, we calculated the height
297 index, width index, doming index, and modeled the surface area of the shell as the lateral area of
298 an ellipsoid cone (Table 2).

299

300 **2.3 Morphometric Analysis**

301 All analyses were performed using R v3.5.1 (R Core Team, 2018) and the tidyverse of
302 packages (Wickham, 2017) and, along with the data, can be found on github:

303 https://github.com/jdselwyn/Opihi_Morphology.

304 For all characters associated with thermal avoidance (i.e. shell surface area, height index
305 and doming index), Bayesian hierarchical regression models were fit to model the relationship
306 between morphology and latitude, as well as the relationship between the morphological
307 variance and the one-dimensional location of each sample, with respect to human habitation. To

308 account for the observation that meso- and microhabitat are generally dominant features shaping
309 shell morphology in patellogastropods (Denny, Dowd, Bilir, & Mach, 2011), sites and islands
310 were treated as hierarchical, random effects on the intercept of shell morphology. All
311 morphological metrics were modeled using a Gaussian response distribution and uninformative
312 priors. Each response variable was fit using four models of increasing complexity (Table 3)
313 which were compared using leave-one-out (loo) and Watanabe-AIC (W-AIC) model weights
314 (Vehtari, Gelman, & Gabry, 2017). The models 1 and 2 only attempted to model the
315 morphological metric of interest while models 3 and 4 additionally modelled the variance in that
316 metric (Table 3). All models were fit using the BRMS implementation of STAN (Gelman, Lee, &
317 Guo, 2015; Bürkner, 2017) with four chains run for 5,000 iterations (1,000 for warm-up).
318 Successful convergence of the chains was assessed using Rhat and visual inspection of traceplots
319 (Vehtari, Gelman, Simpson, Carpenter, & Bürkner, 2019).

320 Upon confirmation of successful model convergence, the best models were chosen based
321 on model weight (Link & Barker, 2006). Global model effects such as a Bayesian equivalent to
322 r^2 were calculated, and individual model coefficients were assessed to determine pairwise
323 differences among islands. Finally, Bayes factors (K), were used to assess the strength of
324 evidence for the *a priori* hypotheses that there is a difference in thermal avoidance and variance
325 in the characters associated with thermal avoidance between uninhabited and inhabited islands
326 and that the effect of latitude is greater in uninhabited than inhabited islands. The strength of
327 evidence (K) for a hypothesis can be negligible (0-3), positive (3-20), strong (20-150), or very
328 strong (>150; Kass & Raftery, 1995). To classify sites according morphometric character traits
329 and their variance, *post hoc* Tukey contrasts were performed among sites with pairs being
330 defined as different if the difference between the posterior means of a given pair did not contain
331 0 within the 95% credible interval. Groupings were labeled alphabetically from highest values on
332 the y- axis (a) to lowest (z).

333

334 **3 RESULTS**

335

336 A total of 402 shells were collected and measured (Table 1). A few shells (3.2%) were
337 missing measurements of L or W due to shell damage. The allometric power model better
338 described the relationship between L and W than a linear model and was used for imputing

339 missing values from damaged shells (Table S1, Figure S1). When normalizing shell
340 measurements for allometry, all of the shells were well described by one allometric relationship
341 for each shell character (W , H , $L_{1,3}$, $C_{1,3}$) and the mean length to which all measurements were
342 normalized was 37 mm (Table S2, Figure S2).

343 There was a bimodal distribution of shell color, where 86% of shells exhibited either
344 <10% or >90% black rib tips (Figure 3). The color morphotypes exhibited a parapatric
345 distribution, with overlap of the two color morphotypes occurring primarily on the central islands
346 (MM, NI, KA; Figures 1 & 3, Table 1), a predominance of light morphotypes on the two most
347 northwestern islands (ON and LA), and a predominance of the dark morphotype on the three
348 most southeastern islands (OA, MA, and HI). On Kaua‘i, there were more light morphs at the
349 site with a calcium carbonate shoreline (29% light, KA2, Table 1), than at the site with a basaltic
350 shoreline (6% light, KA1).

351 The best models of the relationships between the morphometric characters associated
352 with thermal avoidance, their variance, latitude, and location (Table 3) were all Full + σ_b which
353 explained 31-42%, 50-58% and 37-52% of the variance in surface area, height, and doming,
354 respectively (Table 4, Figures 4 & 5).

355 ‘Opihi on the uninhabited NWHI islands had significantly taller ($K = 72$, $p_{\text{posterior}} = 0.99$)
356 and more domed shells ($K = 46$, $p_{\text{posterior}} = 0.98$) with greater surface areas ($K = 56$, $p_{\text{posterior}} =$
357 0.98) despite residing at higher latitudes (Figure 4, Table S3). The differences in surface area
358 were primarily governed by differences in height, with 5x more range in height index than width
359 index (Figure 6). Additionally, the morphometric indices associated with thermal avoidance
360 (shell surface area, height index, and doming index) had different relationships with latitude on
361 uninhabited versus inhabited islands (respectively, $K = 17$, 17, 18 and $p_{\text{posterior}} = 0.94$, 0.94, 0.95;
362 Table S3). Specifically, on uninhabited islands, surface area, height, and doming increased as
363 latitude decreased with a posterior probability of a positive slope being between 0.92 and 0.96
364 (Table 5), but there was either no significant relationship or a negative relationship with latitude
365 on the inhabited islands with 65-85% posterior probability of the slopes being negative. The
366 estimated changes in surface area, doming, and height per degree decrease in latitude on the
367 uninhabited islands were 1.2 cm², 0.014, and 0.030, respectively. On the inhabited islands, there
368 was some support for a slight decrease in the doming index and height index of -0.0046 and -
369 0.016 per degree of latitude, respectively. The slight decreases in all three morphometric

370 character traits in the MHI were due to Kaua‘i having significantly taller, more domed shells
371 with greater surface area than the other three islands (Figure 4). The morphometric characters did
372 not significantly differ between sites within islands (KA1, KA2; OA1, OA2; Figure 4).

373 ‘Opihi on the uninhabited NWHI islands had significantly greater variance in shell
374 surface area ($K = 4.5$, $p_{\text{posterior}} = 0.82$), height ($K = 729$, $p_{\text{posterior}} = 1.0$), and doming ($K = 4166$,
375 $p_{\text{posterior}} = 1.0$; Figure 5, Table S3). There was a significant difference between the inhabited and
376 uninhabited islands in the relationship between the shell doming variance and location ($K = 21$,
377 $p_{\text{posterior}} = 0.96$; Table S3), with a 97% posterior probability of a positive slope in the NWHI and
378 an 89% posterior probability of a negative slope in the MHI (Table 5). While there were not
379 significant differences in the relationships of surface area and height with location between
380 inhabited and uninhabited islands, there was a trend of decreasing variance in shell height with
381 increasing distance from the uninhabited islands, with 76% posterior probability of a negative
382 slope. There were no significant differences in the variance in shell characters between sites
383 within the same islands (Figure 5).

384

385 **4 DISCUSSION**

386

387 **4.1 Incipient Lineage Bifurcation**

388 Together, the parapatric and bimodal distribution of shell coloration (Figures 1, 3) and
389 the disjunct pattern of shell shape (Figure 5) are indicative of lineage bifurcation. Bimodally-
390 distributed, extreme phenotypes exhibiting a parapatric pattern are classic indicators of disruptive
391 and/or bi-directional selection and partial reproductive isolation (Futuyma, 2013; Gauthier,
392 Lumaret, & Bédécarrats, 1998). Disruptive selection favors extreme phenotypes over
393 intermediates (Rueffler., Dooren, Leimar, & Abrams, 2006), and both extremes in coloration
394 with a small proportion of intermediates occur on some islands (Figure 3). On Kaua‘i, the light-
395 colored shells are more common on light than dark substratum. Of the other islands with both
396 calcium carbonate and basalt substratum, *C. exarata* is not known to occur on the calcium
397 carbonate atoll portion of Lalo, Ni‘ihau cannot be accessed due to private ownership, and O‘ahu
398 exhibits no population of light-colored shells (but one individual was observed at the basalt
399 collection site). On the other hand, shell shape, which is somewhat decoupled from shell color

400 (Figures 3b, 4), seems to be experiencing directional selection in opposite directions on the
401 human inhabited MHI versus the uninhabited NWHI.

402 The hypothesis of parapatric lineage diversification is also supported by gene flow
403 estimates between the NWHI and MHI sites (0.02 - 0.77 migrants per generation, mtDNA, Bird
404 et al., 2007) as well as estimates of population genetic structure ($F_{CT} \sim 0.16$, RADseq, Cockett,
405 2015). Passive larval dispersal simulations for marine taxa in Hawai'i also identify a gene flow
406 restriction somewhere between Kaua'i and Mokumanamana (Toonen et al., 2011; Wren,
407 Kobayashi, Jia, & Toonen, 2016).

408 In contrast to the population genetic analyses, a phylogenetic analysis of both mtDNA
409 (12S, 16S, COI) and nDNA (atps β , H3) found no indications of lineage bifurcation in *C. exarata*
410 (Bird et al., 2014). For comparison, the sibling taxon, *C. talcosa*, exhibited a one bp fixed
411 difference in cytochrome C oxidase I between Kaua'i and the other MHI which was dated to
412 ~ 2000 ya (Bird et al., 2011). In *C. exarata*, there either has not been enough time for the genetic
413 lineages to sort, or gene flow is sufficient to prevent lineage sorting in loci that are not strongly
414 affected by disruptive or bi-directional selection. The greater shell surface area and height on
415 Kaua'i relative to the other MHI (Figure 4) may be driven by ongoing gene flow from the
416 NWHI. Overall, the available data support that *C. exarata* is in the early stages of lineage
417 bifurcation.

418 Given our nascent understanding of the processes driving speciation in tropical marine
419 organisms (Bowen, Rocha, Toonen, & Karl, 2013), Hawaiian *Cellana* could serve as a broadly
420 relevant exemplar for marine broadcast-spawners because the majority of marine invertebrates
421 and fishes have dispersive planktonic larvae, but unlike most of these species, the lineage is
422 actively radiating in a tractable historic and geographic context in the Hawaiian archipelago
423 (Bird et al., 2011). The *Cellana* lineage is responding to selective pressures that have clearly and
424 easily observable effects on phenotype (Bird, 2011; Bird et al., 2011) and relevance for
425 adaptation to climate change. Further study of the evolution of Hawaiian *Cellana* would also
426 improve our understanding of why marine radiations and lineage diversification are rare in the
427 Hawaiian archipelago (see Kay & Palumbi, 1987; Wainwright, 2015) and which species would
428 be expected to be diversifying.

429

430 **4.2 Reduced Morphometric Variance on Inhabited Islands: Selection or Bottleneck?**

431 The pattern of depressed morphometric variance on the inhabited MHI is consistent with
432 increased directional selection on morphology and/or a population bottleneck. There appears to
433 be strong selection for flatter shells on the inhabited islands, and this may constrain phenotypic
434 variance in the shell surface area and height index. The phenotypes of limpets and other slow-
435 moving intertidal ectotherms are known to be plastic (Kemp & Bertness, 1984; Teske, Barker, &
436 McQuaid, 2007; Trussell, 1996), and there are typically greater differences across
437 microgeographic rather than latitudinal scales (Denny et al., 2011; Lathlean, McWilliam, Ayre,
438 & Minchinton, 2015; Seabra, Wethey, Santos, & Lima, 2011). At least some proportion of the
439 variation in morphology within and between sites is likely due to plasticity. However, the
440 observed depressed morphometric variance on inhabited islands is unlikely to be due to plasticity
441 because we see no likely stimulus to trigger differential gene expression resulting in the
442 population being more uniformly flat and dark on inhabited islands. Another explanation which
443 does not involve selection and has much more evidentiary support is a population bottleneck.

444 Based upon a genome-wide survey of ~21k SNPs, *C. exarata* exhibited greater genomic
445 diversity on Nihoa (~4.7 km of linear habitat) than on any of the MHI (109-407 km of linear
446 habitat, i.e. larger populations), suggesting that the MHI populations had all experienced a severe
447 bottleneck (Cockett, 2015). The morphometric data presented here exhibit a similar pattern, and
448 therefore it is possible that reduced genetic diversity and morphological variance in the MHI is at
449 least partially due to a historical bottleneck. However, population bottlenecks do not necessarily
450 reduce the capacity to respond to selective pressures (Bryant & Meffert, 1993), especially given
451 the plasticity of limpet shell shape in response to environmental conditions (Teske et al., 2007).
452 To decipher between the effects of genetic variation and selection on the observed patterns in
453 phenotypic variance, it would be necessary to identify and interrogate quantitative trait loci
454 (Wadgyamar et al., 2017). Nonetheless, there are inferences that can be made about the role of
455 selection on the observed phenotypes based upon the available data.

456

457 **4.3 Adaptive Tradeoff: Thermal Regulation and Predation Avoidance**

458 We propose that the pattern of tall, light-colored shells on higher latitude, uninhabited
459 islands and flat, dark-colored shells on lower latitude, inhabited islands is caused by an adaptive
460 tradeoff between thermal and predation avoidance. In response to increasing thermal stress,
461 shells were expected to have greater surface area and be taller, which was observed with

462 decreasing latitudes on the uninhabited islands, consistent with the Iberian limpet *Patella*
463 *depressa* (Hines et al., 2017). However, darker shells which increase the absorbance of solar
464 irradiation, and thus body temperature (Miller & Denny, 2011), became more prevalent with
465 decreasing latitude on both the uninhabited and inhabited islands. The substratum upon which *C.*
466 *exarata* resides is mostly dark basalt across its range, and thus darker shells were more
467 camouflaged (except on the emergent coral reef at Kekaha, Kaua‘i), suggesting an adaptation to
468 visual predators (Merilaita, Scott-Samuel, & Cuthill, 2017). In contrast to color which changes
469 gradually, shells abruptly become flatter on the inhabited islands, and while they cannot dissipate
470 as much heat, it is more difficult and less efficient to apply lateral force that would dislodge or
471 crush these flatter shells (Denny, 2000). We propose that the shells on inhabited islands are
472 colored and shaped to avoid detection and dislodgement by predators at the expense of thermal
473 avoidance.

474 The observed morphometric patterns are consistent with both the homogenizing effects of
475 gene flow from the uninhabited islands and selection. As mentioned above, gene flow from the
476 tall-shelled Nihoa population may be opposing selection against tall shells on Kaua‘i, explaining
477 why the ‘opihī on Kaua‘i are intermediate in height, surface area, and doming between the
478 uninhabited island of Nihoa to the northwest and the densely-populated island of O‘ahu to the
479 southeast. In genetic swamping, geneflow overwhelms the effects of selection acting on a portion
480 of a population (Duputié, Massol, Chuine, Kirkpatrick, & Ronce, 2012). Here, it seems that gene
481 flow is weak enough and selection is strong enough to prevent complete swamping and leading
482 to migration-selection balance as is observed in rock pocket mice (Hoekstra, Drumm, &
483 Nachman, 2004). It also seems likely that geneflow between the NWHI and MHI could be
484 further limited by selection against migrant phenotypes. Identifying the source of selection in the
485 MHI and how it relates to human inhabitation could help to illuminate the dynamics at play.

486

487 **4.4 Is Human Harvesting Driving the Adaptive Tradeoff?**

488 We are compelled by the available evidence to propose that in the past 900-1100 years
489 (~900-2200 generations for *C. exarata*; see Kay & Magruder, 1977) selective pressures applied
490 by humans in the MHI may have driven the distinct biogeographic patterns in the morphology of
491 *C. exarata* reported here, but more investigation is necessary to make a definitive conclusion.
492 ‘Opihī are intensely harvested today (Tom, 2011) and anthropologic studies show that ‘opihī are

493 a consistent staple of the Hawaiian diet (e.g., Kirch et al., 2003; McCoy, 2008; McCoy & Nees,
494 2013; Morrison & Hunt, 2007; Rogers & Weisler, 2019). At an archaeological site on Moloka‘i
495 where *Cellana spp.* were identified to species, *C. exarata* made up 15-60% of the shells (Rogers
496 & Weisler, 2019). Light-colored, tall shells on black rocks are certainly easier to spot than dark,
497 flat shells, especially on heterogeneous shores with shaded crevices, and thus there would be a
498 selective advantage to being less conspicuous. While we have been unable to uncover details on
499 how ‘opihi were harvested prior to European contact, it is possible that taller shells were easier to
500 dislodge and may have been and continue to be favored over flatter shells. Harvest pressure by
501 humans was likely to have been highest in the MHI where the vast majority of the population
502 resided. In the NWHI, only Nihoa was settled by a small number of humans (Emory, 1928). A
503 lack of drinking water would preclude settlement further to the northwest, but Mokumanamana
504 was visited. Since 1815, the entire Hawaiian population has resided in the MHI (Kikiloi et al.,
505 2017). If human colonization of the Hawaiian archipelago is driving the observed adaptive
506 tradeoff in *C. exarata*, then we expect that shells from archaeological sites will become taller
507 with greater surface area with age. We know of no archaeological studies, however, where
508 measurements of shell height or surface area were made because previous efforts focused on
509 shell abundance and/or length (see Kirch et al., 2003; Morrison & Esh, 2015; Morrison & Hunt,
510 2007; McCoy, 2008; Rogers & Weisler, 2019).

511 Alternative predators from the terrestrial realm are birds, rats, and mongoose. Common
512 avian consumers of limpets such as oystercatchers and gulls (Lindberg, Warheit, & Estes, 1987;
513 Marsh, 1986) are mostly absent from Hawai‘i (Harrison, 1990; Henshaw, 1900; Sibley &
514 McFarlane, 1968). There are three extant bird species in Hawai‘i that might prey upon ‘opihi
515 (*Numenius tahitiensis*, *Tringa incana*, and *Arenaria interpres*). They have small bills that are
516 generalized for harvesting smaller invertebrates than adult ‘opihi (Bent, 1929; Dann, 2005;
517 Marshall, 1980) but probably consume juvenile ‘opihi if given the chance. Indeed, *Arenaria*
518 *interpres* has been documented to prey upon limpets but they are not abundant (Whitfield, 1985).
519 Further, none of the extinct birds in the current fossil record seem capable of preying upon
520 limpets (see James & Burney, 1997; Olson & James, 1982). While we cannot rule out that
521 predation on early life stages is driving the observed patterns, we have made additional
522 observations that do not support this hypothesis. For example, we have observed a handful of *C.*
523 *exarata* shells that change color from dark to light with age. Therefore, the requisite genetic

524 variation exists to have dark juveniles that change shell color to light, but this is rarely observed.
525 In fact, a somewhat opposite coloration pattern is observed in the MHI where juveniles tend to
526 have speckled dark and light shell coloration, presumably in response to predation by the
527 aforementioned birds capable of consuming ‘opihi in Hawai‘i, and a more uniform dark
528 coloration as the shell grows larger. Ultimately, crypsis in larger shells in response to predation
529 on larger ‘opihi is the best explanation at present for the predominance of dark-shelled
530 phenotypes when lighter shells would provide an advantage in avoiding thermal stress.

531 The Pacific rat, *Rattus exulans*, was introduced by the Polynesians (Athens, Rieth, &
532 Dye, 2014) and the Europeans later brought *Rattus rattus* and *Rattus norvegicus* as early as 1778
533 (Matisoo-Smith et al., 1998). While the Pacific rat has had the longest opportunity to affect the
534 ‘opihi populations, we have only observed rats in ‘opihi habitat at one location since 1998 (CEB,
535 pers. obs.). The mongoose, *Herpestes javanicus*, has been observed in ‘opihi habitat on
536 numerous occasions (CEB, pers. obs.), but was not introduced to Hawai‘i until 1883 to control
537 rats (Hays & Conant, 2007). While the distribution of these introduced predators on the inhabited
538 MHI correlates with the biogeographic patterns in ‘opihi morphology, there have only been
539 ~150-250 years since their arrival, and there is no modern record of a drastic change in the
540 morphology of *C. exarata*.

541 For the remaining visual marine predators (octopi, fish, and crabs), there does not seem to
542 be a correlation between their abundance and the morphology of ‘opihi. *Cellana exarata*
543 generally resides above the grasp of fishes’ jaws (Bird, Franklin, Smith, & Toonen, 2013) and
544 contemporary fish concentrations are higher in the NWHI than the MHI due to decreased fishing
545 pressure (Friedlander & DeMartini, 2002). The only intertidal octopus in Hawai‘i, *Octopus*
546 *oliveri*, has been commonly observed on intertidal community surveys of Nihoa and
547 Mokumanamana in the uninhabited NWHI (CEB, pers. obs.) as well as in the MHI, and the same
548 is the case with intertidal crabs (e.g., *Grapsus tenuicrustatus*, *Carpillus maculatus*, *Plagusia*
549 *depressa tuberculata*).

550 An alternative hypothesis is that the taller mountains in the MHI cause more cloud cover,
551 decreasing solar irradiance, and thermal stress thereby reducing selection against flatter shells.
552 However, we find it unlikely that increased cloud cover would strongly select for darker shells
553 and against taller shells with greater surface area. Additionally, the same calm weather
554 conditions that result in thermal stress events for *C. exarata*, which resides above the high tide

555 line and depends on waves for immersion (Bird et al., 2013) and cooling, also result in reduced
556 cloud formation above the high islands (Whiteman, 2000).

557

558 **4.5 Implications for Management: Thermal Niche**

559 *Cellana spp.* are over-exploited and the biogeographic pattern described here indicates
560 that most of the *C. exarata* population, which resides in the MHI, is being further constrained by
561 evolutionary forces. While explicit data on the thermal tolerances of *C. exarata* with respect to
562 morphotype and geography do not exist and are beyond the scope of the effort presented here,
563 inferences made from work with limpets in California (Denny, Miller, & Harley, 2006; Dong,
564 Miller, Sanders, & Somero, 2008; Miller, Harley, & Denny, 2009) lead us to predict that in the
565 NWHI, *C. exarata* can inhabit hotter microhabitats, and in the MHI, the population is more
566 dependent upon thermal refugia. The thermal niche breadth of *C. exarata* conferred by shell
567 morphology is narrower in the MHI (inferred using the model described by Denny, 2006), which
568 likely results in reduced habitat exploitation and population size, especially as Earth warms in
569 the tropics (Payne & Smith, 2017). Increasing air temperatures associated with global warming
570 can further constrain the thermal niche. Physiological acclimation (Pintor, Schwarzkopf, &
571 Krockenberger, 2016) or adaptations that increase thermal tolerance could counteract the
572 increased body temperatures caused by flatter shells and warming climate, but the vertical extent
573 of *C. exarata* is presumably at least partially limited by its thermal tolerance (Somero, 2002),
574 leaving little room for additional tolerance in the gene pool. Further, acclimation is unlikely to
575 buffer the additional stress from global warming (Gunderson & Stillman, 2015) and could be
576 investigated in this system where thermal stress increases as latitude decreases.

577 Given that human harvesting is affecting ‘opihi populations and may be contributing to
578 the flatter morphology, it is possible that harvest regulations could alter present selective
579 pressures. More research is required to link harvesting and flat shells, but if there is a causal link,
580 then encouraging or regulating harvest based upon shell height could allow taller morphotypes to
581 proliferate.

582

583 **4.6 Conclusions**

584 While testing for biogeographic patterns in genotype is a typical practice among
585 molecular ecologists, there is still much to be learned from patterns in phenotype and, ideally,

586 investigations of biogeography should employ both. We tested for biogeographic patterns in the
587 morphology of shells in an intertidal ectotherm and found distinct biogeographic patterns in
588 adaptations to predation and temperature, signifying an adaptive tradeoff. These patterns in
589 phenotype illuminated previous population and phylogenetic studies and have helped to identify
590 a population in the early stages of splitting in response to partial isolation and selection. *Cellana*
591 are among the only marine species to have diversified in the Hawaiian archipelago (Bird et al.,
592 2011), and this study identifies one mechanism by which diversification has occurred: parapatry
593 and ecological diversification. We also identified a potential unintended evolutionary
594 consequence of exploitation that negatively affects the long-term sustainability of the fishery by
595 reducing the breadth of the thermal niche dimension. Consequently, knowledge of evolutionary
596 processes is necessary for effective resource conservation and management.

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597 **Table 1.** Summary of sampling locations, dates of human habitation (N = not inhabited), year of sampling, and sample sizes (n) of live
 598 *C. exarata*. The number of dark-colored shells (n_{drk}), light-colored shells (n_{lgt}), and shells requiring the imputation of either length or
 599 width (n_{imp}) are also listed. NWHI is the Northwestern Hawaiian Islands and MHI is the Main Hawaiian Islands.

Region	Island	Code	Site	Dates of	Substratum	Year of	n	n_{drk}	n_{lgt}	n_{imp}
				Human		Sampling				
				Habitation						
				(A.D.) *						
NWHI	‘Ōnū	ON	Nui	N	Basalt	2016	30	0	30	1
	Lalo	LA	Nui	N	Basalt	2016	21	3	18	0
	Mokumanamana	MM	West Cove	N	Basalt	2012	79	33	46	2
	Nihoa	NI	Adams Bay	1400-1815	Basalt	2013	49	38	11	3
Subtotal							179	74	105	6
MHI	Kaua‘i	KA1	Miloli‘i	940-Present	Basalt	2013	33	31	2	4
		KA2	Kekaha	940-Present	CaCO ₃	2013	65	46	19	6
	O‘ahu	OA1	Kaka‘ako	940-Present	Basalt	2013	23	23	0	3
		OA2	Aina Moana	940-Present	Basalt	2013	29	28	1	3
	Maui	MA	Hāna	940-Present	Basalt	2014	26	26	0	1
	Hawai‘i	HI	Hilo	940-Present	Basalt	2013	47	47	0	3
Subtotal							190	170	20	16
Total							402	275	127	26

600 *Athens, Rieth, & Dye, 2014; Kikiloi et al., 2017

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602 **Table 2.** Formulas used to calculate shell indices and estimate surface area. See Figure 2 for
 603 descriptions of the measurement variables.

604

Characters	Formula
Shell Apex	$H_{ai} = \frac{H}{L}$
Height Index	
Shell Aperture	$W_{ai} = \frac{W}{L}$
Width Index	
Shell Doming Index	$D_i = \frac{C_{1,3}}{L_{1,3}}$
Shell Surface Area*	$A_s \cong \frac{1}{2} \int_0^{2\pi} \sqrt{L^2 W^2 H^2 [L^2 \sin^2(t) + W^2 \cos^2(t)]} dt$

* modelled as ellipsoid cone

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609 **Table 3.** Four models were compared to explain the variation in the morphometric characters
 610 shell surface area, height index and doming index (y). Model 1 represents no relationship. The
 611 additional models tested for the effect of human presence, latitude, their interaction, island
 612 (random), and site within islands (random) assuming either equal variances (s , Model 2),
 613 variances related to island and site (Model 3), or variances related to human presence,
 614 geographic isolation (Location), island, and site (Model 4).

Model ID	Model Name	Model Structure
1	Null	$y \sim 1$ $s \sim 1$
2	Full	$y \sim \text{Humans} + \text{Latitude} + (\text{Humans} * \text{Latitude}) + \text{Island} + \text{Site}(\text{Island})$ $s \sim 1$
3	Full + σ_a	$y \sim \text{Humans} + \text{Latitude} + (\text{Humans} * \text{Latitude}) + \text{Island} + \text{Site}(\text{Island})$ $s \sim \text{Island} + \text{Site}(\text{Island})$

4 Full + $y \sim \text{Humans} + \text{Latitude} + (\text{Humans} * \text{Latitude}) + \text{Island} + \text{Site}(\text{Island})$
 σ_b $s \sim \text{Humans} + (\text{Humans} * \text{Location}) + \text{Island} + \text{Site}(\text{Island})$

615

616

617

618 **Table 4.** Model fitting results for surface area, doming index, and height index. The models are
 619 defined in Table 3. loo-ic is the leave one out information criterion, and lower values generally
 620 indicate a better fit. The models with the highest weights were considered the best (bold). The
 621 95% credible interval for r^2 is $CI_{95} r^2$.

Modeled Character	Model Name	loo		
		loo-ic	weights	$CI_{95} r^2$
Surface Area	Null	1528.5	0	0
	Full	1362.3	0.037	0.30-0.42
	Full + σ_a	1296.1	0	0.31-0.42
	Full + σ_b	1295.8	0.963	0.31-0.42
Doming Index	Null	-1864.4	0	0
	Full	-2107.5	0.037	0.41-0.52
	Full + σ_a	-2208.4	0.189	0.38-0.53
	Full + σ_b	-2209.1	0.775	0.37-0.52
Height Index	Null	-1016.4	0	0
	Full	-1311.2	0	0.49-0.58
	Full + σ_a	-1424.8	0.288	0.50-0.58
	Full + σ_b	-1425.2	0.712	0.50-0.58

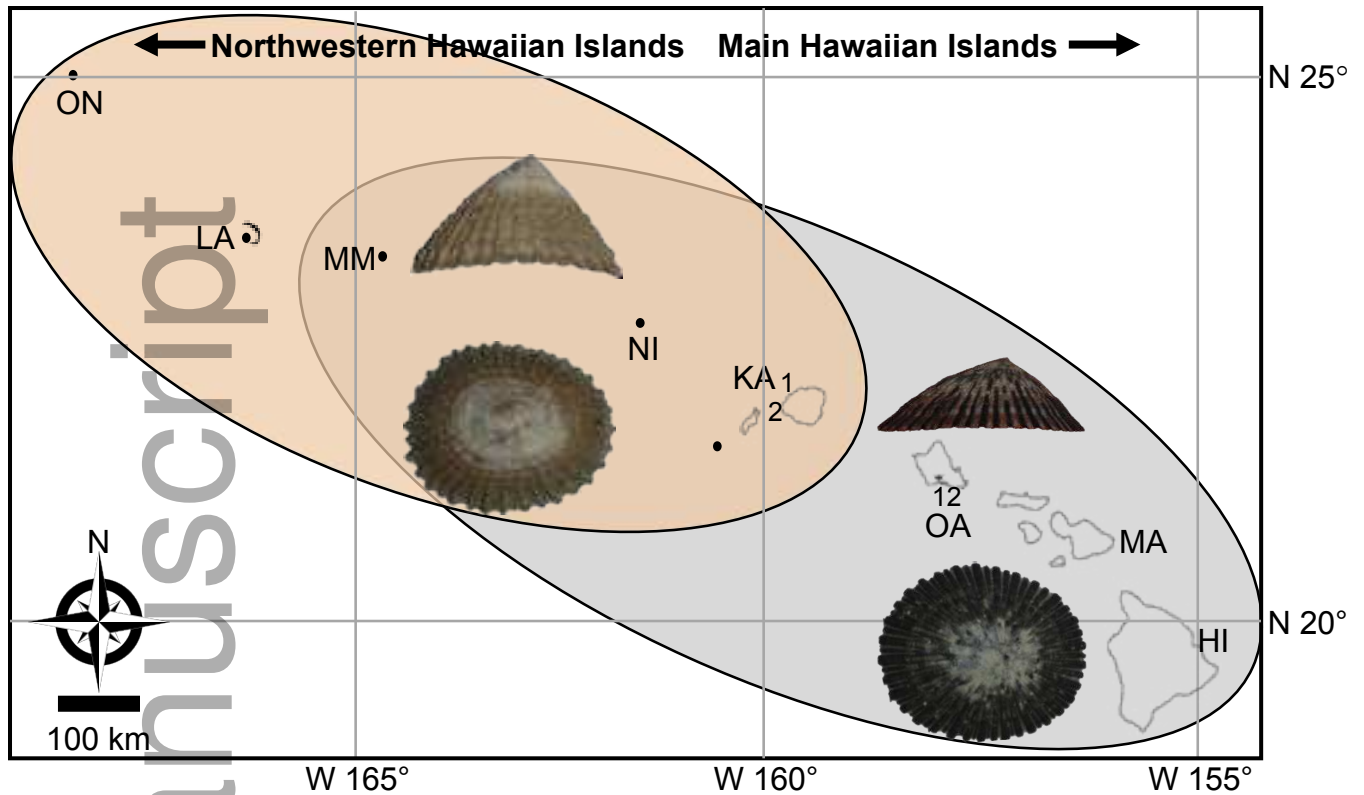
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624 **Table 5.** Summary of slopes modelled for (1) surface area, doming index, and height index versus latitude on uninhabited
 625 Northwestern Hawaiian Islands (NWHI) and inhabited Main Hawaiian Islands (MHI), and (2) the variance in these morphometric
 626 characters versus geographic location. Bolding indicates slopes with a posterior probability >75% .

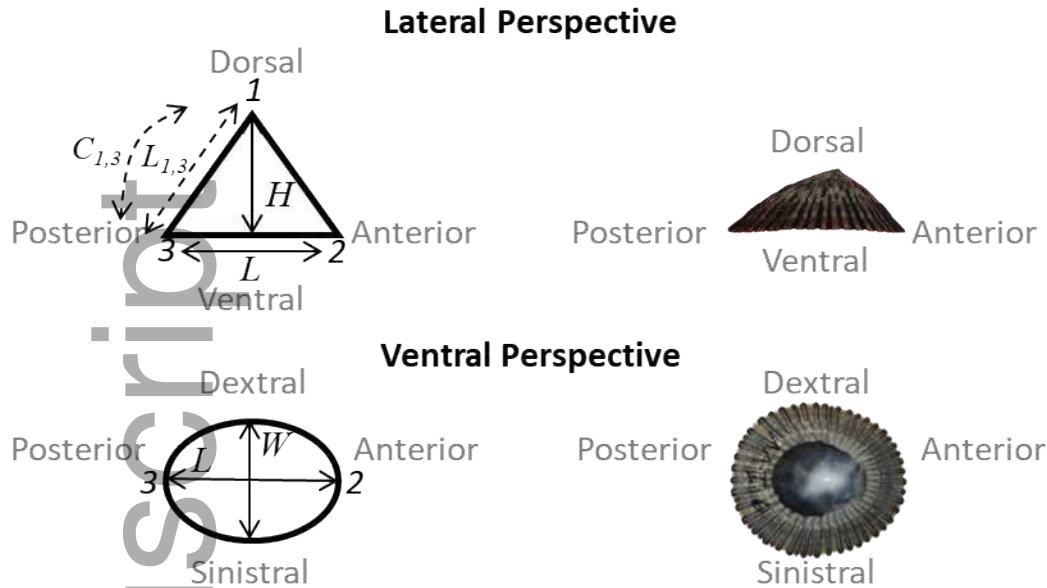
Region	Character	Median			Posterior	Posterior
		Slope (Change per Degree)	Upper 95% CI	Lower 95% CI	Probability of Positive Slope	Probability of Negative Slope
NWHI	Surface Area (cm ²)	1.15E+00	2.53E+00	-2.29E-01	0.957	0.0427
	Doming Index	1.45E-02	3.55E-02	-5.57E-03	0.947	0.0527
	Height Index	2.97E-02	7.65E-02	-1.88E-02	0.922	0.0784
	Variance in Surface Area (cm ²)	-5.22E-05	1.96E-03	-2.04E-03	0.528	0.472
	Variance in Doming Index	-1.15E-03	9.96E-06	-2.36E-03	0.974	0.0265
	Variance in Height Index	1.82E-04	1.99E-03	-1.67E-03	0.394	0.606
MHI	Surface Area	-1.62E-01	9.33E-01	-1.21E+00	0.349	0.651
	Doming Index	-4.56E-03	1.19E-02	-2.04E-02	0.218	0.782
	Height Index	-1.55E-02	2.19E-02	-5.08E-02	0.147	0.853
	Variance in Surface Area (cm ²)	-6.40E-04	4.85E-03	-6.19E-03	0.629	0.371
	Variance in Doming Index	1.55E-03	4.84E-03	-1.74E-03	0.107	0.893
	Variance in Height Index	1.32E-03	6.43E-03	-3.72E-03	0.24	0.76

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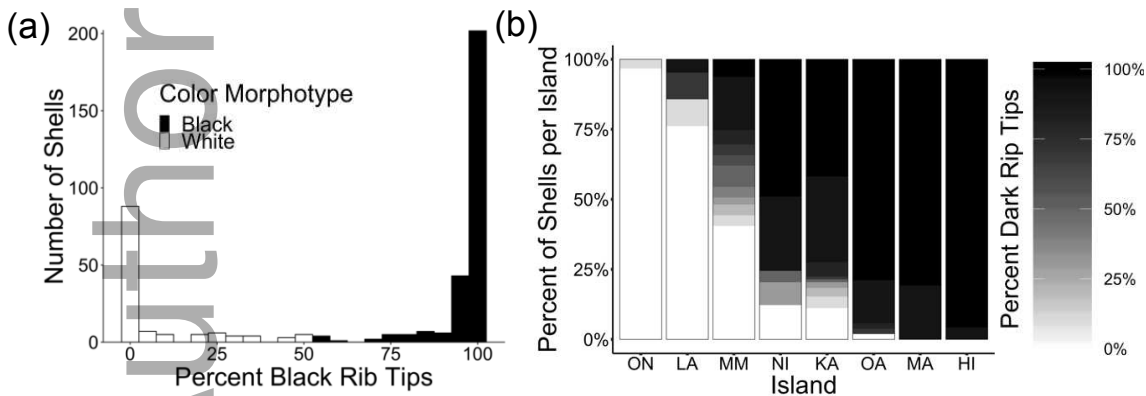


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Figure 1. Map of the Hawaiian Archipelago. Sampling sites are labeled by either the island abbreviation or, when there were multiple sites, the site number (as described in Table 1). The biogeographic range of color morphotypes observed in the samples is represented by the filled ovals (peach – lighter shells, grey – darker shells). A photograph of an example shell of each color morphotype from a ventral and dorsal perspective is shown near the islands typically harboring those morphs.

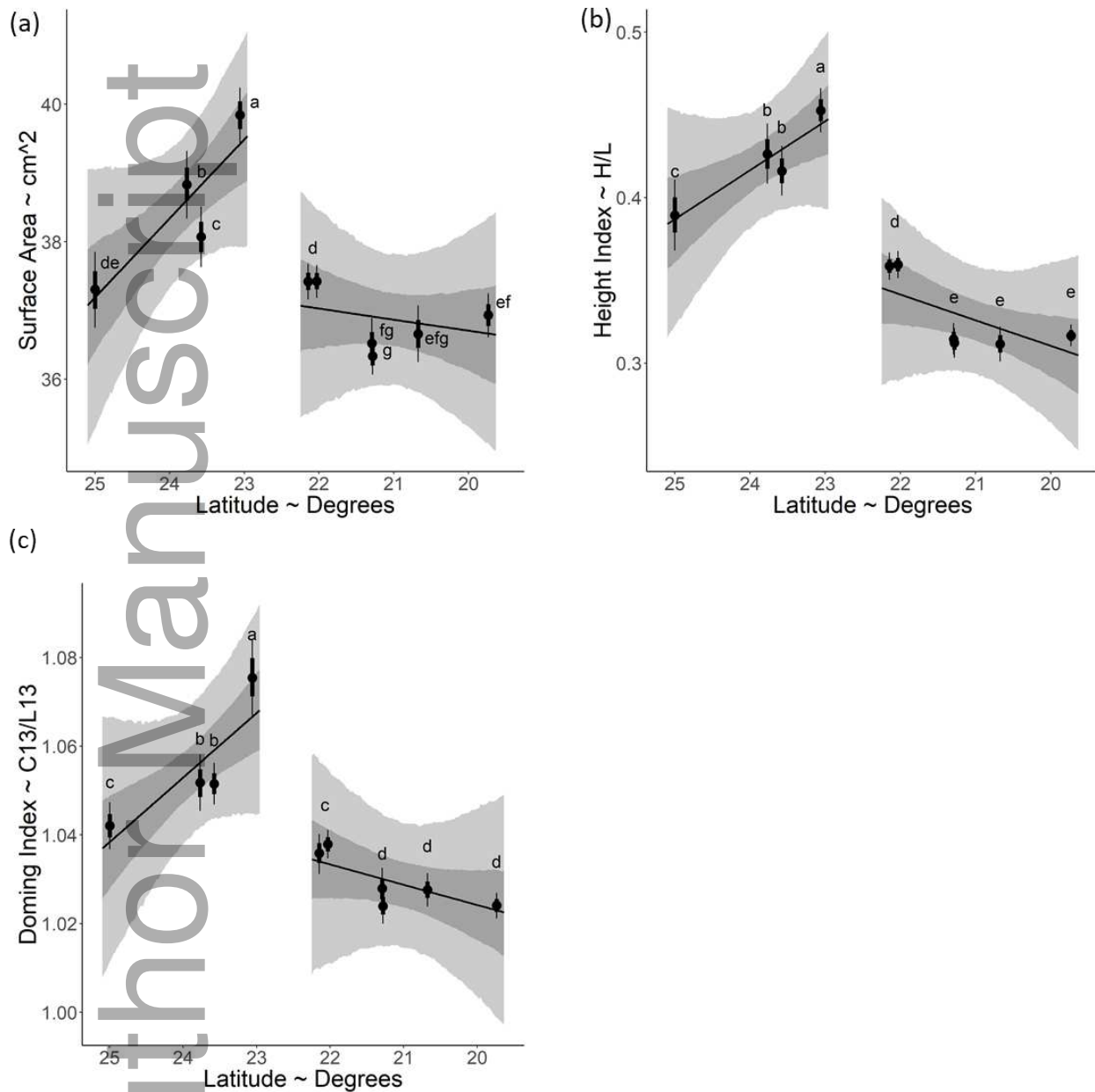


640
 641 **Figure 2.** Diagram of shell measurements and landmarks from lateral and ventral perspectives
 642 with matching photographs of shells for context. The numbers represent Cartesian coordinates
 643 obtained from photographs, and the letters represent characters: L = length, W = width, C =
 644 distance following the edge of the shell which was generally curvilinear. Solid lines represent
 645 measurements made with calipers, and dashed lines represent measurements made using
 646 photographs.
 647



648
 649 **Figure 3.** Histogram of the number of shells that had a given percentage of darkly pigmented rib
 650 tips (a), and a bar plot depicting the proportion of shells per island classified based on the percent
 651 of dark rib tips in 10% bins. Darker colors indicate a greater percent dark rib tips and lighter
 652 colors indicate a smaller percent dark rib tips. It should be noted that KA represents two sites and
 653 the site with lightly colored CaCO_3 substratum (KA2) had a higher proportion of light shells

654 than the other site with dark basalt substratum (KA1). All other sites had dark basalt substratum
655 (Table 1).

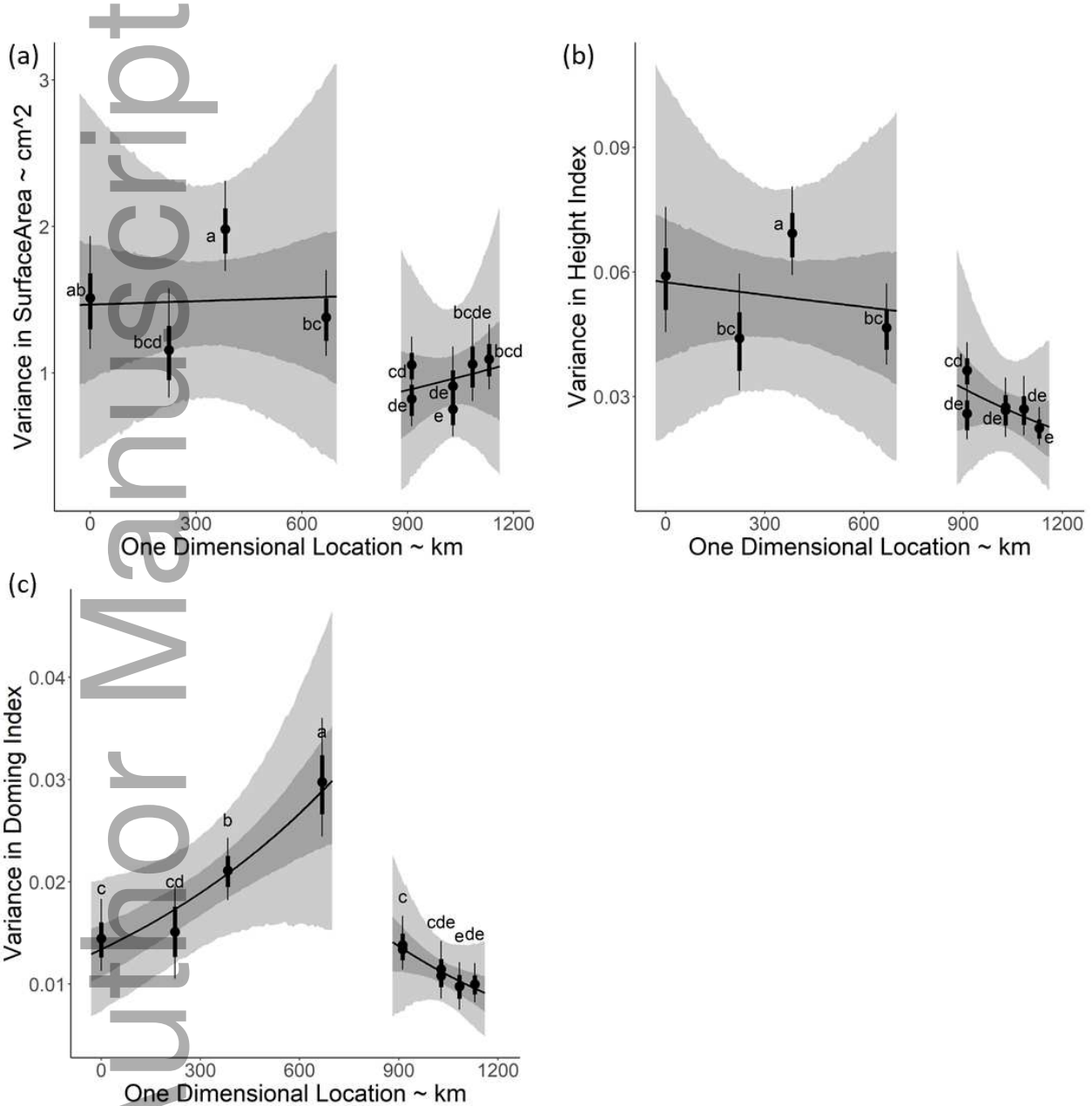


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658 **Figure 4.** Scatterplots of (a) surface area, (b) height index, and (c) doming index versus latitude.
659 Points are the median observed values and error bars represent 68% (thick) and 95% (thin)
660 credible intervals. Regression lines represent the best-fit model of the medians with dark grey
661 ribbons showing the 68% credible interval and the light grey ribbons representing the 95%
662 credible intervals. The letters in each panel represent statistical groupings based on pairwise

663 Tukey tests among site coefficients as determined by the model. Sites with differing grouping
664 letters had significant differences in the means. If sites within the same island have one letter,
665 they were in the same grouping.

666

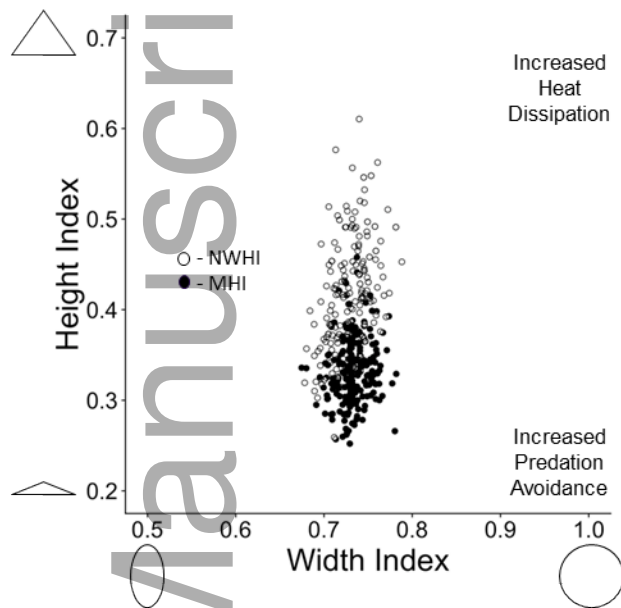


667

668 **Figure 5.** Scatter plots of the variances in (a) surface area, (b) height index, and (c) doming
669 index versus the one-dimensional stepping-stone location which is related to isolation (Bird et
670 al., 2007). Points are the median observed values and error bars represent 68% (thick) and 95%
671 (thin) credible intervals. Regression lines represent the best-fit model of the medians with dark

672 grey ribbons showing the 68% credible interval and the light grey ribbons representing the 95%
673 credible intervals. The letters in each panel represent statistical groupings based on pairwise
674 Tukey tests among site coefficients as determined by the model. Sites with differing grouping
675 letters had significant differences in the means. If sites within the same island have one letter,
676 they were in the same grouping.

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679

680 **Figure 6.** Scatter plot of shell height index versus width index for all shells. Triangles on y-axis
681 represent lateral shell profile dimensions and the ellipse and circle on the x-axis represent the
682 aperture dimensions. Heat dissipation through the shell is maximized at a width index of 1 and a
683 larger height index. Predation avoidance due to apex crushing and laterally applied forces is
684 maximized at a width index of 1 and a smaller height index. Note that the range of both axes is
685 0.5 to accurately depict the broader distribution of heights than widths.

686

687

688 **DATA AVAILABILITY**

689

690 All data and images analyzed here are published on DRYAD (Hamilton et al., 2020), and the
691 scripts used for data processing and analysis are published on GitHub
692 (https://github.com/jdselwyn/Opihi_Morphology).

693

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991

992

993 **BIOSKETCHES**

994

995 Ashley M. Hamilton is an undergraduate student who is broadly interested in evolutionary
996 biology and the mechanisms of selection. Her work focuses on the phenotypic and genetic
997 patterns associated with evolutionary change in a variety of systems, with a special focus on
998 plant systems.

999
1000 Jason D. Selwyn is interested in the causes and consequences of variations in dispersal
1001 dynamics. His research focuses on understanding the environmental factors leading to
1002 dispersal variation in Caribbean reef gobies.

1003
1004
1005 Rebecca M. Hamner has broad interests in conservation biology, molecular ecology, and
1006 evolution. Her current work focuses on applying genomic tools to answer questions related to the
1007 conservation and management of threatened and culturally important species.

1008
1009 Hoku Johnson is interested in human uses of the nearshore environment and indigenous
1010 connections to place, focusing on Native Hawaiian gathering practices, local stewardship of
1011 marine resources, and ways state and federal regulations influence community health.

1012
1013 Tia Brown is interested in Hawaii's marine ecosystems, particularly nearshore and intertidal
1014 ecosystems science. Her focus centers on ways to weave traditional Hawaiian knowledge and
1015 practices together with modern-day science and technology to maintain the health, beauty, and
1016 wealth of Hawaii's natural resources and serve as a model for the rest of the world.

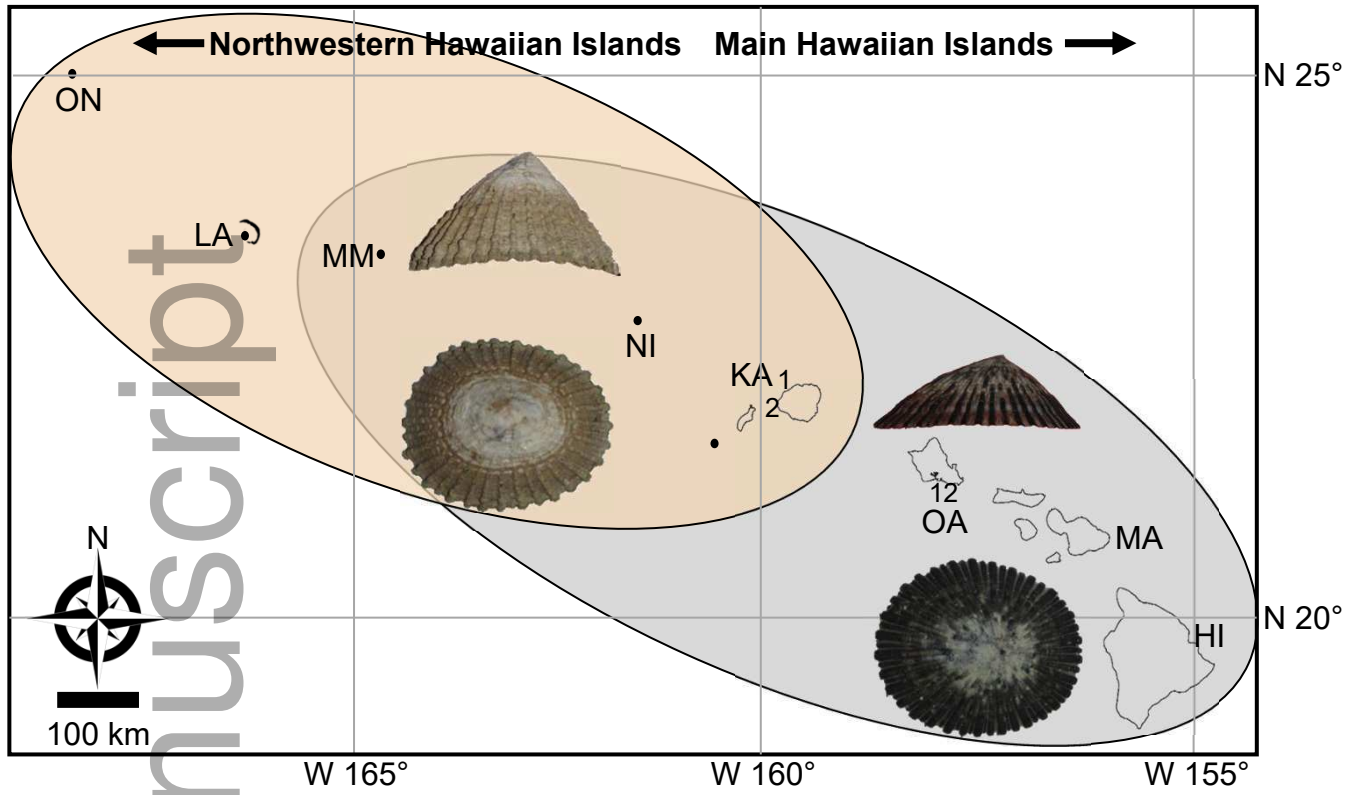
1017
1018 Shauna Kēhaunani Springer is interested intertidal and nearshore ecosystems. She focuses on
1019 understanding and incorporating traditional Hawaiian monitoring and customary practices into
1020 her research and building community capacity around these efforts.

1021
1022 Christopher E. Bird is an Associate Professor that uses molecular and computational tools to
1023 study the evolution of marine life on ecological time scales to facilitate marine resource
1024 management and conservation.

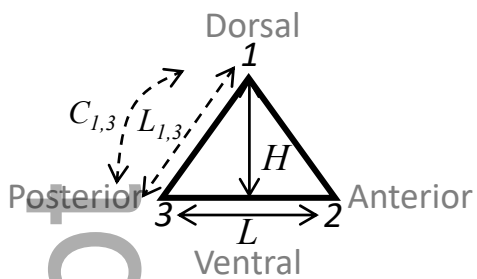
1025

1026 **Author contributions:** Project conception: CEB. Sample collection: HKJ, TB, KS, CEB;
1027 Character state scoring: AMH, RMH, HKJ, TB, KS, CEB; Data processing and analysis: AMH,
1028 RMH, JDS, CEB; Writing and editing: all authors.

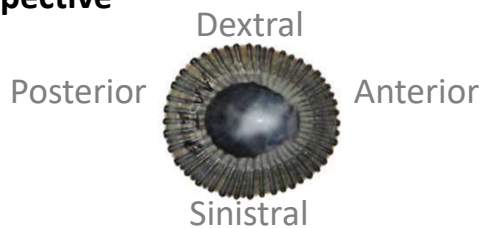
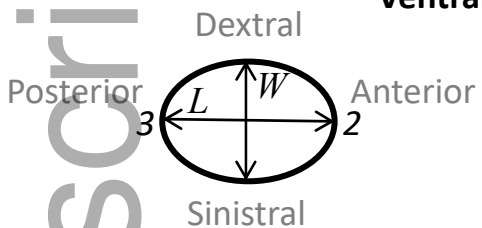
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