RESEARCH PAPER

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

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Abstract

Aim: Humans are unintentionally affecting the evolution of fishery species directly through exploitation and indirectly by altering climate. We aim to test for a relationship between biogeographic patterns in the shell phenotypes of an over-exploited shellfish and the presence of humans to identify human-mediated adaptive trade-offs. The implications of these trade-offs are discussed with respect to the sustainability of the fishery.

Taxon: The endemic Hawaiian intertidal limpet, 'opihi makaiauli (Patellagastropoda, Nacellidae, Cellana exarata)

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

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

Main Conclusions: The biogeographic patterns in shell phenotype and previous genetic studies suggest that the population is beginning to bifurcate in response to disruptive and directional selection as well as geographic isolation between the islands with and without humans. Decreased phenotypic and genetic diversity on the inhabited islands despite much larger populations of 'opihi suggests a prominent historical bottleneck. The prevalence of maladaptive dark, flat phenotypes for thermal avoidance on the inhabited islands suggests that predation is a stronger selective force, driving adaptive trade-offs in shape and colour. We propose that this is likely a case of fisheries-induced evolution and a millennium of harvesting is the most likely selective pressure driving the observed biogeographic patterns in shell morphology. The flatter, darker shells will

allow body temperatures to rise higher in direct sunlight, therefore we hypothesize that the thermal niche of 'opihi is narrower on inhabited islands and will continue to narrow as Earth warms.

1 | INTRODUCTION

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

The extent of phenotypic variation and limits on the adaptation of any single phenotype are governed by the effects of adaptive trade-offs on the overall fitness of an organism (reviewed in Agrawal, Conner, & Rasmann, 2010). A single-trait trade-off occurs when multiple selective pressures affect a single phenotype, preventing the maximization of fitness in response to any one of the multiple selective pressures. Single-trait trade-offs can lead to polymorphisms when selective pressures vary in space due to either local adaptation or phenotypic plasticity (Agrawal et al., 2010; Futuyma, 2013). For example, the shell thickness of the intertidal snail *Littorina obtusata* covaries with predation pressure at the expense of body mass and, presumably, physiological maintenance of the organism (Trussell, 2000).

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

Two strong selective pressures that are influenced by humans and vary across biogeographic space are temperature and predation. (a) Temperatures generally increase with decreasing latitudes, increased exposure to solar irradiance, and can drive adaptations to tolerate or avoid stressful conditions, especially in ectotherms (Verheyen & Stoks, 2019). Temperatures are also increasing in conjunction with rising levels atmospheric carbon dioxide (Snyder, 2016), pushing ectotherms closer to their thermal limits (Pinsky, Eikeset, McCauley, Payne, & Sunday, 2019). Adaptations in ectotherms enabling thermal regulation and avoidance can be effective in ameliorating thermal stress. For example, ectotherms can seek thermal refuges (Dillon, Liu, Wang, & Huey, 2012) or employ behaviours that modulate temperature (Miller & Denny, 2011; Seuront & Ng, 2016). Morphological features, such as shell size and shape in gastropod snails, can affect the body's heat budget (Denny & Harley, 2006; Harley, Denny, Mach, & Miller, 2009), and lighter coloration can decrease the absorbance of solar irradiation which can result in decreased body temperature (Geen & Johnston, 2014; Pereboom & Biesmeijer, 2003; Trullas, van Wyk, & Spotila, 2007). (b) Predation is often correlated with other habitat and environmental characteristics (Beukers & Jones, 1998), and in edible species, proximity to humans can be an important predictor (Cinner, Graham, Huchery, & MacNeil, 2013; Williams et al., 2008). Adaptations in response to predation include a decrease in mean body size (Meiri, 2008; Ratner & Lande, 2001; Trussell, 2000), increased frequency of protective characters (Caley & Schluter, 2003; Leonard, Bertness, & Yund, 1999; Trussell, 2000) and cryptic coloration (Merilaita, Lyytinen, & Mappes, 2001; Miller & Denny, 2011). For example, mussels have been shown to exhibit an increase in shell strength and more tightly attach to substrate due to predation (Leonard et al., 1999).

In intertidal ectotherms, such as patellogastropods, both predation and thermal stress can be intense (Branch, Trueman, & Clarke, 1985; Knight, 2011; Lowell, 1984; Vermeij, 1973). Under thermally stressful conditions which occur during periods of emersion and direct solar irradiance in the middle of the day, lighter-coloured, taller shells with greater surface area are advantageous in limiting thermal and desiccation stresses (inferred from Denny & Harley, 2006). Lighter colours reflect solar irradiation (Miller & Denny, 2011); shells with greater surface area can shed more heat to the atmosphere (Denny & Harley, 2006); and taller shells can experience greater wind velocities, aiding in heat dissipation (Harley et al., 2009), while

absorbing the same amount of solar irradiation as shorter shells with less surface area (calculated from Pennell & Deignan, 1989, see Denny & Harley, 2006). Indeed, a pattern of increasing shell height with decreasing latitude was observed in the limpet, *Patella depressa*, on the Iberian peninsula (Hines et al., 2017).

Flatter, cryptically coloured shells, however, are advantageous in avoiding predation, setting up a potential trade-off with morphologies that ameliorate thermal stress (Hines et al., 2017). Predators such as fishes and crabs cannot prey as efficiently on flatter-shelled limpets because both crushing the shell apex (Lowell, 1986; Vermeij, 1973) and applying lateral force for dislodgement is more difficult. Cryptically coloured shells that blend into the background are also more difficult for predators to detect (Miller & Denny, 2011) and is an important mechanism of survival for intertidal gastropods (Manríquez, Lagos, Jara, & Castilla, 2009). Sorensen and Lindberg (1991) concluded that *Lottia pelta* limpets with less cryptic shell coloration were more commonly consumed by American black oyster catchers (*Haematopus bachmani*), and Mercurio, Palmer, and Lowell (1985) employed experimental transplants to demonstrated that cryptic coloration results in lower rates of predation in the limpet, *Collisella digitalis*, by both fishes and birds.

The over-exploited, endemic Hawaiian limpets, *Cellana* spp., provide an ideal opportunity to test for adaptive trade-offs in shell morphology where thermal stress and predation are negatively correlated. *Cellana exarata*, locally known as ʻopihi makaiauli, are high-intertidal, endemic, monecious broadcast-spawners with a 2–14 day pelagic larval duration. *Cellana exarata* ranges along a latitudinal and thermal gradient from ʻŌnū (Gardner Pinnacles, 25° N) to the Big Island of Hawaiʻi (19° N) where the morphology transitions from light-coloured and tall-shelled to dark-coloured and flat-shelled (Kay & Schoenberg-Dole, 1991). All of the islands are predominantly composed of dark basaltic substratum, which makes lighter, solar irradiance-reflecting shell colours disadvantageous in the face of predation pressure, while darker shells are more camouflaged from predators. In the hotter Main Hawaiian Islands (MHI, Kauaʻi – Hawaiʻi), ʻopihi have been intensely harvested (Kay & Magruder, 1977; McCoy, 2008) ever since they were colonized, AD 940–1130 (Athens, Rieth, & Dye, 2014). The uninhabited, cooler Northwestern Hawaiian Islands (NWHI) are subject to lower predation pressure since all but one of these islands (Nihoa) have never been settled by humans (Kikiloi et al., 2017) and they are presently within the Papahānaumokuākea Marine National Monument where harvest by humans is largely illegal. Further, the NWHI harbouring ʻopihi are small (<69 ha) and devoid of terrestrial predators capable of consuming adult ʻopihi such as rats and mongooses.

The Hawaiian archipelago provides ample opportunity for physical and genetic isolation among islands (Toonen et al., 2011), which can foster local adaptation (Blondel, 2008). Indeed, there are gene flow restrictions in *C. exarata* among islands with varying levels of genetic isolation across the archipelago (Bird, Holland, Bowen, & Toonen, 2007; Cockett, 2015). Importantly, the most pronounced genetic isolation is found between the uninhabited NWHI and inhabited MHI. Cockett (2015) also found that genomic diversity decreased, on average, from the smaller populations in the NWHI to the

larger populations in the MHI, a signature of a historical population bottleneck. Despite these genetic patterns and morphological differences between the NWHI and MHI ʻopihi, genetic investigations have been unable to identify species-level differentiation (Samollow, pers. comm. [allozymes]; Reeb, 1995 [mtDNA]; Bird, Holland, Bowen, & Toonen, 2011 [mtDNA and nDNA]; Cockett, 2015 [RADseq]).

Here we conduct the first rigorous investigation of the biogeography of shell morphology and coloration in *C. exarata* across the entire species range. We test for a decline in morphometric variation from the NWHI to the MHI that parallels the genetic pattern reported by Cockett (2015). We hypothesized that if thermal and desiccation stress were the dominant selective pressures affecting *C. exarata*, then shells would be progressively lighter-coloured and taller with greater surface area down the latitudinal gradient. We test this hypothesis on both the inhabited and uninhabited islands to test for a competing effect of predation on the adaptation of ʻopihi to thermal stress. If predation is the most important selective pressure, then we expect that shells would be flatter and darker, making the ʻopihi more difficult to detect and dislodge from the substratum. We conclude by discussing the observed biogeographic patterns and the potential role of humans in the evolution of ʻopihi.

2 | MATERIALS AND METHODS

2.1 | Sample collection and geographic metadata

Living and presumably healthy *Cellana exarata* were collected from eight Hawaiian Islands between 2012 and 2016: ʻŌnū (ON, Gardner Pinnacles, Puha honu), Lalo (LA, La Perouse Pinnacles, Mokupāpapa), Mokumanamana (MM, Necker), Nihoa (NI), Kauaʻi (KA), Oʻahu (OA), Maui (MA) and Hawaiʻi (HI, Big Island; Table 1; Kikiloi et al., 2017). The NWHI were accessed during intertidal monitoring cruises sponsored by Papahānaumokuākea Marine National Monument, and eight ʻopihi were collected from each of six, 1 cm size classes. In the MHI, shells of legal harvesting size (>3 cm) were haphazardly collected along a 7 km section of coastline on Maui, two locations on Kauaʻi (Miloliʻi and Kekaha) and Oʻahu (Kakaʻako, ʻĀina Moana) and one location on each of the remaining islands. All sites were composed of natural basalt formations with the exceptions of the Oʻahu and Hawaiʻi sites (basalt riprap) and Kekaha (emergent coral reef). Site selection was largely haphazard because shell morphology (at the level investigated here) was observed to be more homogenous within than between the NWHI and MHI. For example, Bird (2011) found very small differences in shell shapes among five disparate locations in the MHI, four of which were on the Big Island of Hawaiʻi. Kekaha, Kauaʻi, however, was deliberately targeted because its light-coloured, emergent coral reef substratum was known to harbour a light-coloured morphotype of *C. exarata*. Overall, there was no meaningful confounding of human habitation, the selection of survey sites within islands and the individuals collected for analysis.

Geographic location information for each sampling site was obtained using Google Earth Pro 7.3.2.5776. The one-dimensional

TABLE 1 Summary of sampling locations, dates of human habitation (*N* = not inhabited), year of sampling and sample sizes (*n*) of live *C. exarata*. The number of dark-coloured shells (n_{drk}), light-coloured shells (n_{lgt}), and shells requiring the imputation of either length or 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 Human Habitation (A.D.)[a]	Substratum	Year of Sampling	*n*	n_{drk}	n_{lgt}	n_{imp}
NWHI	ʻŌnū	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	Kauaʻi	KA1	Miloliʻi	940–Present	Basalt	2013	33	31	2	4
		KA2	Kekaha	940–Present	CaCO₃	2013	65	46	19	6
	Oʻahu	OA1	Kakaʻako	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
	Hawaiʻi	HI	Hilo	940–Present	Basalt	2013	47	47	0	3
	Subtotal						190	170	20	16
Total							402	275	127	26

[a]Athens et al. (2014); Kikiloi et al. (2017).

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

2.2 | Character state scoring, missing data imputation and allometric normalization

The newest parts of the shell (rib tips) were used to classify shell colour based upon the expression of dark periostracum, the proteinaceous shell coating and irrespective of shell erosion. Rib tip colour was scored estimating the percentage of rib tips that had dark pigment in increments of 25% in each of four quadrants and averaging the scores for each shell. If ≥50% of rib tips were dark, the colour morphotype of the shell was classified as dark-coloured. Otherwise the shell was classified as light-coloured.

We were primarily interested in investigating morphometric characters related to thermal avoidance: shell surface area and shell height.

TABLE 2 Formulas used to calculate shell indices and estimate surface area. See Figure 1 for descriptions of the measurement variables

Characters	Formula
Shell apex height index	$H_{ai} = \frac{H}{L}$
Shell aperture width index	$W_{ai} = \frac{W}{L}$
Shell doming index	$D_i = \frac{C_{1,3}}{L_{1,3}}$
Shell surface area[a]	$A_s \cong \frac{1}{2} \int_0^{2\pi} \sqrt{L^2 W^2 H^2 \left[L^2 \sin^2(t) + W^2 \cos^2(t) \right]} \, dt$

[a]Modelled as ellipsoid cone.

We measured shell height (*H*), length (*L*) and width (*W*) directly using dial calipers and inferred surface area by modelling the shell as an ellipsoid cone (Table 2). Because the lateral area of a cone does not account for shell doming, we calculated a doming index based upon the lateral length from the apex to posterior margin of the aperture along the axis of symmetry in the shortest distance possible ($L_{1,3}$) and along the curve of shell's surface ($C_{1,3}$, Figure 1) using ImageJ (Schneider, Rasband, & Eliceiri, 2012) and images taken from the lateral perspective (see Figure 1). Landmarks defined by cartesian coordinates were placed on either end of a size standard, the apex (Point 1), the anterior (Point 2) and posterior aperture edge (Point 3). The lengths ($L_{1,3}$, $L_{2,3}$) were calculated using the Pythagorean Theorem, while $C_{1,3}$ was determined by drawing a line using the segmented line tool from point 1 to 3 along each shell's edge, and then converted to mm using the size standard. Finally, a scale correction factor to align ImageJ measures with those from the calipers was determined by dividing L_i by $L_{2,3i}$, where *i* is each individual's identity and was multiplied by $L_{1,3i}$ and $C_{1,3i}$.
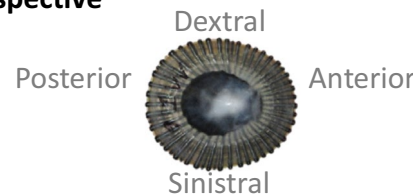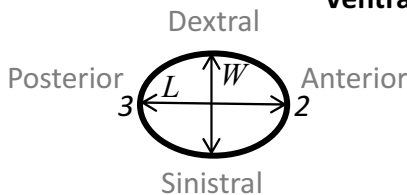
Lateral Perspective
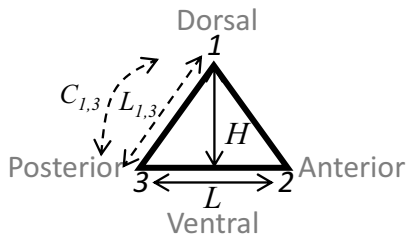
Ventral Perspective

FIGURE 1 Diagram of shell measurements and landmarks from lateral and ventral perspectives with matching photographs of shells for context. The numbers represent the Cartesian coordinates obtained from photographs, and the letters represent characters: L = length, W = width, C = distance following the edge of the shell which was generally curvilinear. Solid lines represent measurements made with calipers, and dashed lines represent measurements made using photographs

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

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

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

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 length, $\bar{L}$ is the mean shell length and a and b are constants (Lleonart, Salat, & Torres, 2000). These relationships were tested as described for the imputations (Table S2). To better satisfy the assumptions of each model, the L and Y were natural log-transformed except in the case of width because all assumptions were met without a transformation (Figure S2). After allometric normalization, all individuals smaller than 25 mm in length were excluded from the study because juveniles tend to have different morphologies from adults due to ontological changes (Vermeij, 1973). From the allometrically normalized measurements, we calculated the height index, width index, doming index and modelled the surface area of the shell as the lateral area of an ellipsoid cone (Table 2).

2.3 | Morphometric analysis

All analyses were performed using R 3.5.1 (R Core Team, 2018) and the TIDYVERSE of packages (Wickham, 2017) and, along with the data, can be found on github: https://github.com/jdselwyn/Opihi_Morphology.

For all characters associated with thermal avoidance (i.e. shell surface area, height index and doming index), Bayesian hierarchical

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

Model ID	Model name	Model structure
1	Null	$y \sim 1$
		$s \sim 1$
2	Full	$y \sim$ Humans+Latitude+(Humans*Latitude)+Island+Site(Island)
		$s \sim 1$
3	Full+σ_a	$y \sim$ Humans+Latitude+(Humans*Latitude)+Island+Site(Island)
		$s \sim$ Island+Site(Island)
4	Full+σ_b	$y \sim$ Humans+Latitude+(Humans*Latitude)+Island+Site(Island)
		$s \sim$ Humans+(Humans*Location)+Island+Site(Island)

regression models were fit to model the relationship between morphology and latitude, as well as the relationship between the morphological variance and the one-dimensional location of each sample, with respect to human habitation. To account for the observation that meso- and micro-habitat are generally dominant features shaping shell morphology in patellogastropods (Denny, Dowd, Bilir, & Mach, 2011), sites and islands were treated as hierarchical, random effects on the intercept of shell morphology. All morphological metrics were modelled using a Gaussian response distribution and uninformative priors. Each response variable was fit using four models of increasing complexity (Table 3) which were compared using leave-one-out (loo) and Watanabe-AIC (W-AIC) model weights (Vehtari, Gelman, & Gabry, 2017). The models 1 and 2 only attempted to model the morphological metric of interest while models 3 and 4

additionally modelled the variance in that metric (Table 3). All models were fit using the BRMS implementation of STAN (Bürkner, 2017; Gelman, Lee, & Guo, 2015) with four chains run for 5,000 iterations (1,000 for warm-up). Successful convergence of the chains was assessed using 'Rhat' and visual inspection of TRACEPLOTS (Vehtari, Gelman, Simpson, Carpenter, & Bürkner, 2019).

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

3 | RESULTS

A total of 402 shells were collected and measured (Table 1). A few shells (3.2%) were missing measurements of L or W due to shell damage. The allometric power model better described the relationship between L and W than a linear model and was used for imputing missing values from damaged shells (Table S1, Figure S1). When normalizing shell measurements for allometry, all of the shells were well-described by one allometric relationship for each shell character (W, H, $L_{1,3}$, $C_{1,3}$) and the mean length to which all measurements were normalized was 37 mm (Table S2, Figure S2).

There was a bimodal distribution of shell colour, where 86% of shells exhibited either <10% or >90% black rib tips (Figure 2). The colour morphotypes exhibited a parapatric distribution, with overlap of the two colour morphotypes occurring primarily on the central islands (MM, NI, KA; Figures 2 and 3, Table 1), a predominance of light morphotypes on the two most northwestern islands (ON and LA), and a predominance of the dark morphotype on the three most southeastern islands (OA, MA and HI). On Kaua'i, there were more light morphs at the site with a calcium carbonate shoreline (29% light, KA2, Table 1), than at the site with a basaltic shoreline (6% light, KA1).

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

'Opihi on the uninhabited NWHI islands had significantly taller ($K = 72$, $p_{posterior} = 0.99$) and more domed shells ($K = 46$, $p_{posterior} = 0.98$) with greater surface areas ($K = 56$, $p_{posterior} = 0.98$) despite residing at higher latitudes (Figure 4, Table S3). The differences in surface area were primarily governed by differences in height, with 5x more range in height index than width index (Figure 6). Additionally, the morphometric indices associated with thermal avoidance (shell surface area, height index and doming index) had different relationships with latitude on uninhabited versus inhabited islands (respectively, $K = 17$, 17, 18 and $p_{posterior} = 0.94$, 0.94, 0.95; Table S3). Specifically, on uninhabited islands, surface area, height and doming increased as latitude decreased with a posterior probability of a positive slope being between 0.92 and 0.96 (Table 5), but there was either no significant relationship or a negative relationship with latitude on the inhabited islands with 65%–85% posterior probability of the
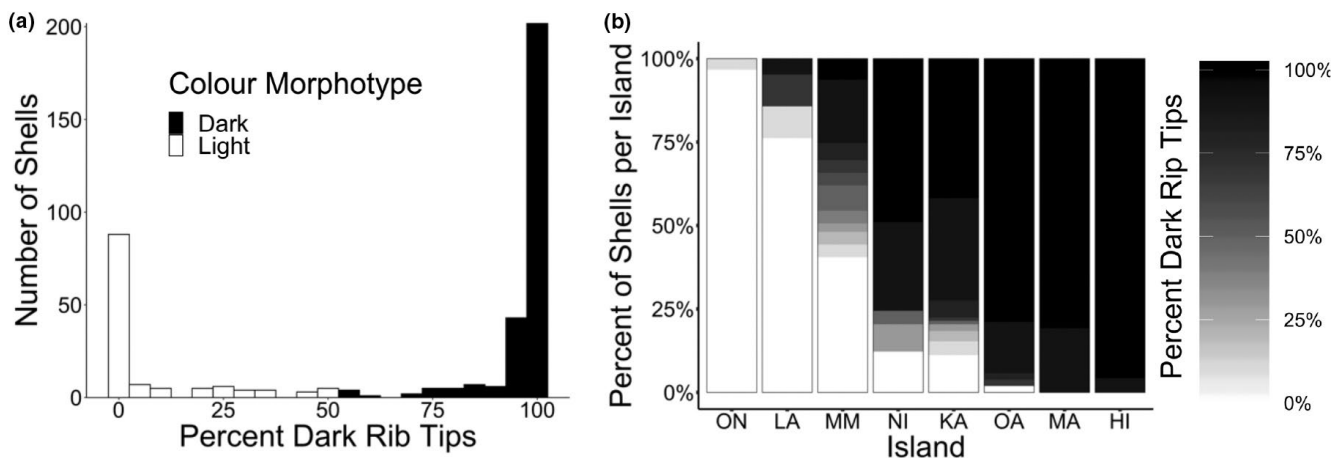

FIGURE 2 Histogram of the number of shells that had a given percentage of darkly pigmented rib tips (a), and a bar plot depicting the proportion of shells per island classified based on the percent of dark rip tips in 10% bins. Darker colours indicate a greater percent dark rib tips and lighter colours indicate a smaller percent dark rib tips. It should be noted that KA represents two sites and the site with lightly coloured CaCO$_3$ substratum (KA2) had a higher proportion of light shells than the other site with dark basalt substratum (KA1). All other sites had dark basalt substratum (Table 1)
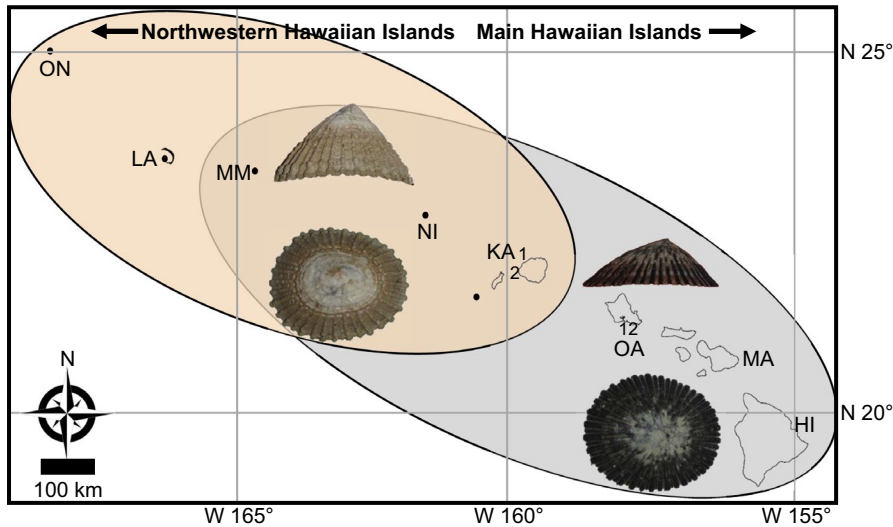
FIGURE 3 Map of the Hawaiian Archipelago. Sampling sites are labelled by either the island abbreviation or, when there were multiple sites, the site number (as described in Table 1). The biogeographic range of colour morphotypes observed in the samples is represented by the filled ovals (peach – lighter shells, grey – darker shells. A photograph of an example shell of each colour morphotype from a ventral and dorsal perspective is shown near the islands typically harbouring those morphs [Colour figure can be viewed at wileyonlinelibrary.com]

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

Modelled character	Model name	loo-ic	loo weights	$CI_{95}\ r^2$
Surface area	Null	1,528.5	0	0
	Full	1,362.3	.037	.30–.42
	Full+σ_a	1,296.1	0	.31–.42
	Full+σ_b	**1,295.8**	**.963**	**.31–.42**
Doming index	Null	−1,864.4	0	0
	Full	−2,107.5	.037	.41–.52
	Full+σ_a	−2,208.4	.189	.38–.53
	Full+σ_b	**−2,209.1**	**.775**	**.37–.52**
Height index	Null	−1,016.4	0	0
	Full	−1,311.2	0	.49–.58
	Full+σ_a	−1,424.8	.288	.50–.58
	Full+σ_b	**−1,425.2**	**.712**	**.50–.58**

slopes being negative. The estimated changes in surface area, doming and height per degree decrease in latitude on the uninhabited islands were 1.2 cm^2, 0.014 and 0.030 respectively. On the inhabited islands, there was some support for a slight decrease in the doming index and height index of −0.0046 and −0.016 per degree of latitude respectively. The slight decreases in all three morphometric character traits in the MHI were due to Kaua'i having significantly taller, more domed shells with greater surface area than the other three islands (Figure 4). The morphometric characters did not significantly differ between sites within islands (KA1, KA2; OA1, OA2; Figure 4).

'Opihi on the uninhabited NWHI islands had significantly greater variance in shell surface area ($K = 4.5$, $p_{posterior} = 0.82$), height ($K = 729$, $p_{posterior} = 1.0$) and doming ($K = 4,166$, $p_{posterior} = 1.0$; Figure 5, Table S3). There was a significant difference between the inhabited and uninhabited islands in the relationship between the shell doming variance and location ($K = 21$, $p_{posterior} = 0.96$; Table S3), with a 97% posterior probability of a positive slope in the NWHI and an 89% posterior probability of a negative slope in the MHI (Table 5). While there were no significant differences in the relationships of surface area and height with location between inhabited and uninhabited islands, there was a trend

of decreasing variance in shell height with increasing distance from the uninhabited islands, with 76% posterior probability of a negative slope. There were no significant differences in the variance in shell characters between sites within the same islands (Figure 5).

4 | DISCUSSION

4.1 | Incipient lineage bifurcation

Together, the parapatric and bimodal distribution of shell coloration (Figures 2 and 3) and the disjunct pattern of shell shape (Figure 5) are indicative of lineage bifurcation. Bimodally distributed, extreme phenotypes exhibiting a parapatric pattern are classic indicators of disruptive and/or bidirectional selection and partial reproductive isolation (Futuyma, 2013; Gauthier, Lumaret, & Bédécarrats, 1998). Disruptive selection favours extreme phenotypes over intermediates (Rueffler, Van Dooren, Leimar, & Abrams, 2006), and both extremes in coloration with a small proportion of intermediates occur on some islands (Figure 2). On Kaua'i, the light-coloured shells are

FIGURE 4 Scatterplots of (a) surface area, (b) height index, and (c) doming index versus latitude. Points are the median observed values and error bars represent 68% (thick) and 95% (thin) credible intervals. Regression lines represent the best-fit model of the medians with dark grey ribbons showing the 68% credible interval and the light grey ribbons representing the 95% credible intervals. The letters in each panel represent statistical groupings based on pairwise Tukey tests among site coefficients as determined by the model. Sites with differing grouping letters had significant differences in the means. If sites within the same island have one letter, they were in the same grouping
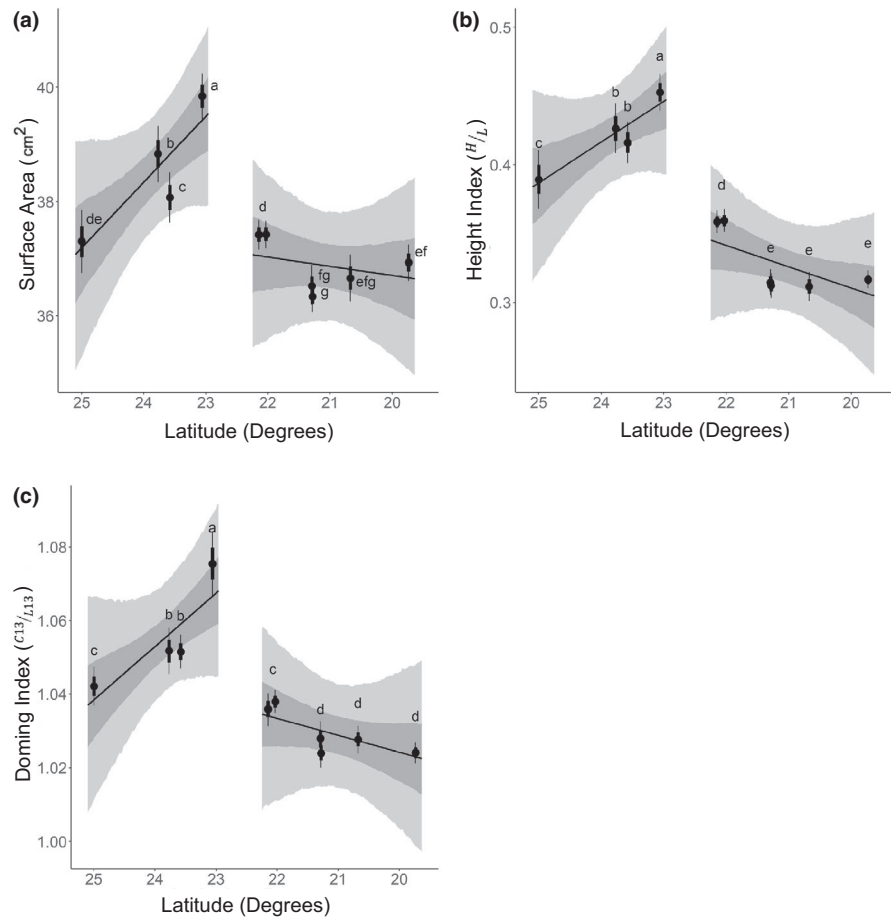
more common on light than dark substratum. Of the other islands with both calcium carbonate and basalt substratum, *C. exarata* is not known to occur on the calcium carbonate atoll portion of Lalo, Niʻihau cannot be accessed due to private ownership, and Oʻahu exhibits no population of light-coloured shells (but one individual was observed at the basalt collection site). On the other hand, shell shape, which is somewhat decoupled from shell colour (Figures 2b and 4), seems to be experiencing directional selection in opposite directions on the human-inhabited MHI versus the uninhabited NWHI.

The hypothesis of parapatric lineage diversification is also supported by gene flow estimates between the NWHI and MHI sites (0.02–0.77 migrants per generation, mtDNA, Bird et al., 2007) as well as estimates of population genetic structure (F_{CT} ~ 0.16, RADseq, Cockett, 2015). Passive larval dispersal simulations for marine taxa in Hawaiʻi also identify a gene flow restriction somewhere between Kauaʻi and Mokumanamana (Toonen et al., 2011; Wren, Kobayashi, Jia, & Toonen, 2016).

In contrast to the population genetic analyses, a phylogenetic analysis of both mtDNA (12S, 16S, COI) and nDNA (atpsβ, H3) found no indications of lineage bifurcation in *C. exarata* (Bird et al., 2011). For comparison, the sibling taxon, *Cellana talcosa*, exhibited a one bp fixed difference in cytochrome C oxidase I between Kauaʻi and the other MHI which was dated to ~2,000 ya (Bird et al., 2011). In *C. exarata*, there either has not been enough time for the genetic lineages to sort, or gene flow is sufficient to prevent lineage sorting in loci that are not strongly affected by disruptive or bidirectional

selection. The greater shell surface area and height on Kauaʻi relative to the other MHI (Figure 4) may be driven by ongoing gene flow from the NWHI. Overall, the available data support that *C. exarata* are in the early stages of lineage bifurcation.

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

4.2 | Reduced morphometric variance on inhabited islands: selection or bottleneck?

The pattern of depressed morphometric variance on the inhabited MHI is consistent with increased directional selection on morphology
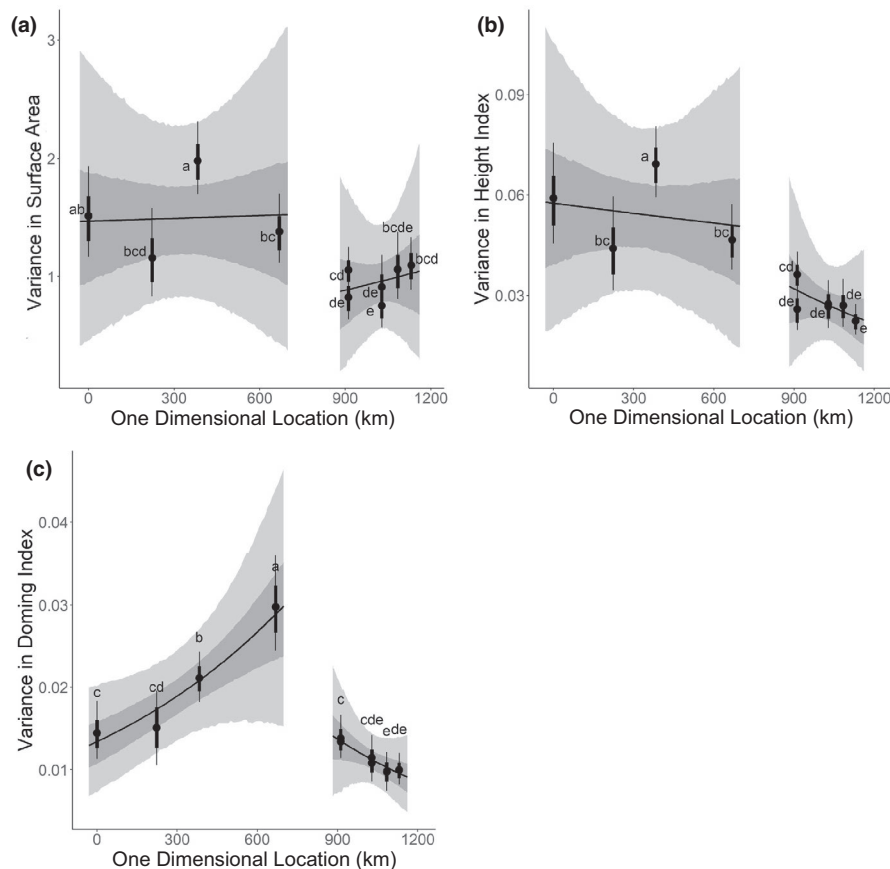
FIGURE 5 Scatter plots of the variances in (a) surface area, (b) height index, and (c) doming index versus the one-dimensional stepping-stone location which is related to isolation (Bird et al., 2007). Points are the median observed values and error bars represent 68% (thick) and 95% (thin) credible intervals. Regression lines represent the best-fit model of the medians with dark grey ribbons showing the 68% credible interval and the light grey ribbons representing the 95% credible intervals. The letters in each panel represent statistical groupings based on pairwise Tukey tests among site coefficients as determined by the model. Sites with differing grouping letters had significant differences in the means. If sites within the same island have one letter, they were in the same grouping

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

Based upon a genome-wide survey of ~21k SNPs, *C. exarata* exhibited greater genomic diversity on Nihoa (~4.7 km of linear habitat) than on any of the MHI (109–407 km of linear habitat, i.e. larger populations), suggesting that the MHI populations had all experienced a severe bottleneck (Cockett, 2015). The morphometric data presented here exhibit a similar pattern, and therefore it is possible that reduced genetic diversity and morphological variance in the MHI is at least partially due to a historical bottleneck. However, population bottlenecks do not necessarily reduce the capacity to respond to selective pressures (Bryant & Meffert, 1993), especially given the

plasticity of limpet shell shape in response to environmental conditions (Teske et al., 2007). To decipher between the effects of genetic variation and selection on the observed patterns in phenotypic variance, it would be necessary to identify and interrogate quantitative trait loci (Wadgymar et al., 2018). Nonetheless, there are inferences that can be made about the role of selection on the observed phenotypes based upon the available data.

4.3 | Adaptive trade-off: thermal regulation and predation avoidance

We propose that the pattern of tall, light-coloured shells on higher latitude, uninhabited islands and flat, dark-coloured shells on lower latitude, inhabited islands is caused by an adaptive trade-off between thermal and predation avoidance. In response to increasing thermal stress, shells were expected to have greater surface area and be taller, which was observed with decreasing latitudes on the uninhabited islands, consistent with the Iberian limpet *P. depressa* (Hines et al., 2017). However, darker shells which increase the absorbance of solar irradiation, and thus body temperature (Miller & Denny, 2011), became more prevalent with decreasing latitude on both the uninhabited and inhabited islands. The substratum upon which *C. exarata* resides is mostly dark basalt across its range, and thus darker shells were more camouflaged (except on the emergent coral reef at Kekaha, Kaua'i), suggesting an adaptation to visual predators (Merilaita, Scott-Samuel,
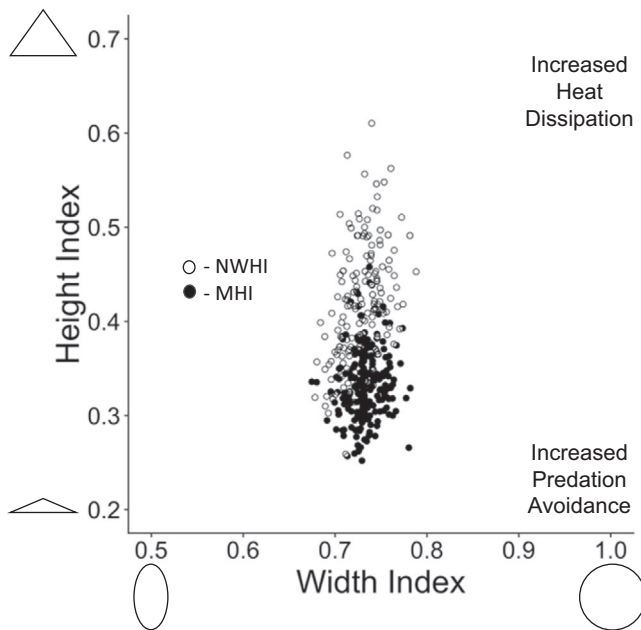
FIGURE 6 Scatter plot of shell height index versus width index for all shells. Triangles on *y*-axis represent lateral shell profile dimensions and the ellipse and circle on the *x*-axis represent the aperture dimensions. Heat dissipation through the shell is maximized at a width index of 1 and a larger height index. Predation avoidance due to apex crushing and laterally applied forces is maximized at a width index of 1 and a smaller height index. Note that the range of both axes is 0.5 to accurately depict the broader distribution of heights than widths

& Cuthill, 2017). In contrast to colour which changes gradually, shells abruptly become flatter on the inhabited islands, and while they cannot dissipate as much heat, it is more difficult and less efficient to apply lateral force that would dislodge or crush these flatter shells (Denny, 2000). We propose that the shells on inhabited islands are coloured and shaped to avoid detection and dislodgement by predators at the expense of thermal avoidance.

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

4.4 | Is human harvesting driving the adaptive trade-off?

We are compelled by the available evidence to propose that in the past 900–1,100 years (~900–2,200 generations for *C. exarata*; see Kay & Magruder, 1977) selective pressures applied by humans in the MHI may have driven the distinct biogeographic patterns in the morphology of *C. exarata* reported here, but more investigation is necessary to make a definitive conclusion. 'Opihi are intensely harvested today (Tom, 2011) and anthropologic studies show that 'opihi are a consistent staple of the Hawaiian diet (e.g. Kirch et al., 2003; McCoy, 2008; McCoy & Nees, 2013; Morrison & Hunt, 2007; Rogers & Weisler, 2019). At an archaeological site on Moloka'i where *Cellana* spp. were identified to species, *C. exarata* made up 15%–60% of the shells (Rogers & Weisler, 2019). Light-coloured, tall shells on black rocks are certainly easier to spot than dark, flat shells, especially on heterogeneous shores with shaded crevices, and thus there would be a selective advantage to being less conspicuous. While we have been unable to uncover details on how 'opihi were harvested prior to European contact, it is possible that taller shells were easier to dislodge and may have been and continue to be favoured over flatter shells. Harvest pressure by humans was likely to have been highest in the MHI where the vast majority of the population resided. In the NWHI, only Nihoa was settled by a small number of humans (Emory, 1928). A lack of drinking water would preclude settlement further to the northwest, but Mokumanamana was visited. Since 1815, the entire Hawaiian population has resided in the MHI (Kikiloi et al., 2017). If human colonization of the Hawaiian archipelago is driving the observed adaptive trade-off in *C. exarata*, then we expect that shells from archaeological sites will become taller with greater surface area with age. We know of no archaeological studies, however, where measurements of shell height or surface area were made because previous efforts focused on shell abundance and/or length (see Kirch et al., 2003; Morrison & Esh, 2015; Morrison & Hunt, 2007; McCoy, 2008; Rogers & Weisler, 2019).

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

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

Region	Character	Median slope (change per degree)	Upper 95% CI	Lower 95% CI	Posterior probability of positive slope	Posterior probability of negative slope
NWHI	Surface area (cm^2)	1.15E + 00	2.53E + 00	−2.29E−01	**.957**	.0427
	Doming index	1.45E−02	3.55E−02	−5.57E−03	**.947**	.0527
	Height index	2.97E−02	7.65E−02	−1.88E−02	**.922**	.0784
	Variance in surface area (cm^2)	−5.22E−05	1.96E−03	−2.04E−03	.528	.472
	Variance in doming index	−1.15E−03	9.96E−06	−2.36E−03	**.974**	.0265
	Variance in height index	1.82E−04	1.99E−03	−1.67E−03	.394	.606
MHI	Surface area	−1.62E−01	9.33E−01	−1.21E + 00	.349	.651
	Doming index	−4.56E−03	1.19E−02	−2.04E−02	.218	**.782**
	Height index	−1.55E−02	2.19E−02	−5.08E−02	.147	**.853**
	Variance in surface area (cm^2)	−6.40E−04	4.85E−03	−6.19E−03	.629	.371
	Variance in doming index	1.55E−03	4.84E−03	−1.74E−03	.107	**.893**
	Variance in height index	1.32E−03	6.43E−03	−3.72E−03	.24	**.76**

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

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

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

An alternative hypothesis is that the taller mountains in the MHI cause more cloud cover, decreasing solar irradiance, and thermal stress thereby reducing selection against flatter shells. However, we find it unlikely that increased cloud cover would strongly select for darker shells and against taller shells with greater surface area. Additionally, the same calm weather conditions that result in thermal stress events for *C. exarata*, which resides above the high tide line and depends on waves for immersion (Bird et al., 2013) and cooling, also result in reduced cloud formation above the high islands (Whiteman, 2000).

4.5 | Implications for management: thermal niche

Cellana spp. are over-exploited and the biogeographic pattern described here indicates that most of the *C. exarata* population, which resides in the MHI, is being further constrained by evolutionary forces. While explicit data on the thermal tolerances of *C. exarata* with respect to morphotype and geography do not exist and are beyond the scope of the effort presented here, inferences made from work with limpets in California (Denny & Harley, 2006; Dong, Miller, Sanders, & Somero, 2008; Miller & Denny, 2011) lead us to predict that in the NWHI, *C. exarata* can inhabit hotter microhabitats, and in the MHI, the population is more dependent upon thermal refugia. The thermal niche breadth of *C. exarata* conferred by shell morphology is narrower in the MHI (inferred using the model described by Denny & Harley, 2006), which likely results in reduced habitat exploitation and population size, especially as Earth warms in the tropics (Payne & Smith, 2017). Increasing air temperatures associated with global warming can further constrain the thermal niche. Physiological acclimation (Pintor, Schwarzkopf, & Krockenberger, 2016) or adaptations that increase thermal tolerance could counteract the increased body temperatures caused by flatter shells and

warming climate, but the vertical extent of *C. exarata* is presumably at least partially limited by its thermal tolerance (Somero, 2002), leaving little room for additional tolerance in the gene pool. Further, acclimation is unlikely to buffer the additional stress from global warming (Gunderson & Stillman, 2015) and could be investigated in this system where thermal stress increases as latitude decreases.

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

4.6 | Conclusions

While testing for biogeographic patterns in genotype is a typical practice among molecular ecologists, there is still much to be learned from patterns in phenotype and, ideally, investigations of biogeography should employ both. We tested for biogeographic patterns in the morphology of shells in an intertidal ectotherm and found distinct biogeographic patterns in adaptations to predation and temperature, signifying an adaptive trade-off. These patterns in phenotype illuminated previous population and phylogenetic studies and have helped to identify a population in the early stages of splitting in response to partial isolation and selection. *Cellana* are among the only marine species to have diversified in the Hawaiian archipelago (Bird et al., 2011), and this study identifies one mechanism by which diversification has occurred: parapatry and ecological diversification. We also identified a potential unintended evolutionary consequence of exploitation that negatively affects the long-term sustainability of the fishery by reducing the breadth of the thermal niche dimension. Consequently, knowledge of evolutionary processes is necessary for effective resource conservation and management.

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BIOSKETCHES

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

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

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

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

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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