

**UNDERSTANDING KŪPE‘E (*NERITA POLITA*) GONAD DEVELOPMENT AND  
DEMOGRAPHY FOR CONTINUED USE AT TWO SITES ON HAWAI‘I ISLAND**

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Mahalo mau a mau to those who have guided this journey, including those who came before me, my ‘ohana, committee members and mentors, and the community we are a part of. May this work provoke curiosity, inspiration, and action. May it be refined, added to, and one day rendered obsolete by the wealth of knowledge and understanding.

Amama ua noa!

## **Abstract**

Kūpe‘e (*Nerita polita* Linnaeus, 1758) is a cryptic, mostly nocturnal intertidal species of gastropod mollusc used widely in Hawai‘i for sustenance and cultural practices. Despite a long tradition of human interaction with this species, information is generally lacking regarding its reproductive ecology. Results of this study suggest that male and female individuals do not differ significantly in size and that the minimum shell length at maturity for both males and females is 14 mm. Mature gonads were present in both sexes throughout the study period, and mating was documented throughout the same period, suggesting continuous spawning throughout the year. These results are consistent at both study sites, Kawaihae and Waiuli, Hawai‘i. Comparison of population size structure at the study sites with the desirable shell lengths, as denoted by the Bishop Museum lei collection and modern lei, shows that less than 5% of the population fits into the desirable size range.

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## Introduction

*Ka i 'a kīnohinohi pōhaku.*

*The fish that adorn the rocks.*

*The periwinkles and nerites that cling to the rocks in shallow water.*

*- 'Ōlelo No 'eau 1354*

Effective species conservation and management requires an understanding of population dynamics and life history characteristics. The 'Ōlelo No 'eau above (Pukui 2001) describes the intimate knowledge Hawaiians had of the animals of the intertidal regions. Today, this type of demographic information may not be frequently obtained for some species, especially those that are nocturnal and utilize lunar cycles (Kronfeld-Schor et al. 2013). The mostly nocturnal intertidal marine gastropod, *Nerita polita*, also known in Hawai'i as kūpe'e, is one such species. Since the purpose of this study is to better understand this species through the lens of perpetuating the continuity of Hawaiian cultural use, the name kūpe'e will be used.

## Morphology

Kūpe'e is member of the family Neritidae. Its domed shell is smooth, growing up to 4cm in length with three to four whorls. It displays a broad range of shell colors and patterns, which is discussed in detail below. The aperture is white, the columella is smooth, and the columellar edge has two to four weak denticles. The calcareous operculum is also smooth, colored cream to black, and there is no umbilicus (Morris 1974).

## Habitat

*He pō Kāloa kēia, ua 'e'e pūpū.*

*This is the night of Kāloa, for the shellfish climbs.*

*The nights of Kāloa, when the shellfish climb onto the wet stones, are good for shellfish hunting.*

*- 'Ōlelo No 'eau 907*

During diurnal high tides, kūpe'e reside under water buried in sand or small rubble near the base of basalt or limestone structures, and emerge when the tide recedes below their burrow to graze on the microalgae and diatoms of nearby boulders, and mate (Hughes 1971; Vermeij 1971). They take advantage of the evening or nocturnal low tide, emerging as soon as possible, and returning underground shortly after their nutritional and/or reproductive activities are finished, even if substantial time remains before the incoming tide reaches their burrow. Over the course of this study it was observed that if the low tide occurred towards the early morning, no kūpe'e would be visible throughout their habitat range, having already retreated underground before the daylight transition took place. It was also noted that on rare occasions at specific locations, kūpe'e may remain visible during daylight hours.

Kūpe'e and other neritids provide ecosystem services through grazing on diatom and other microalgae populations, and they contribute to intertidal erosion and habitat transition through the scraping of their radula during grazing (Chelazzi 1982; Murphy and Underwood 2006). Habitat with light to moderate exposure to wave activity is most suitable for kūpe'e (Hughes 1971).

### ***Distribution***

Kūpe'e are part of the genus *Nerita*, one of the most prominent tropical intertidal groups of the Indo-West Pacific (Estabrooks, Kay, and McCarthy 1999; Frey and Vermeij 2008),

ranging from eastern Africa, between continental Asia and Australia, and across the Pacific to Tahiti, Hawai‘i, and into the north, including Japan. Their broad distribution is likely due to extended periods, sometimes several months, spent as planktonic larvae, which is undocumented in this species, but characteristic of *Nerita* (Giovas et al. 2013; Page and Ferguson 2013), supporting the broad species dispersal.

### ***Predation***

Intertidal species are subject to predation from both land and sea. Crepuscular and nocturnal species are optimally situated to prey upon kūpe‘e. Data on kūpe‘e predation specifically are lacking, however, it is likely that they experience similar marine predation as other intertidal invertebrates, including from carnivorous snails, crabs, eel, octopus and lobster. Terrestrial predators could include feral cats, mongoose (*Herpestes javanicus*), birds that hunt coastally in the evenings or at night, such as the aukū‘u (*Nycticorax nycticorax hoactli*), and of course, humans.

### ***Edible Kūpe‘e***

*Ka i ‘a kīnohinohi pōhaku.*

*The fish that adorn the rocks.*

*- ‘Ōlelo No ‘eau 1354*

Perhaps our oldest connection to kūpe‘e is as mea‘ai, or food. In Hawai‘i, some people eat kūpe‘e raw, others boiled, and others still with their own “secret” recipes. In Tonga, a distinction is made between similar species as such, “we eat the ones that come out of the sand, not the ones on the rocks” (Kalei, pers. comm.). In Kiribati, Micronesia, they are called *te kaban*, the general name for neritids, and they are gathered along with a diverse molluscan population

and eaten (F. R. Thomas 2001). Kūpe'e comprise a large proportion of nerite remains in middens in Tutuila, American Samoa (Morrison and Addison 2008).

Middens across Hawai'i show that kūpe'e were consumed at much lower rates (as measured by both number of individual shells and shell weight) than pipipi (*N. picea*), which made up a large proportion of the molluscan part of the diet. At Wai'ahukini in Ka'u, kūpe'e were found throughout the oldest to the most recent cultural layers, representing 330±30 years BP (before present) to historic times, but in consistently lower numbers than other molluscs (Emory and Bonk 1969; Lundblad et al. 2014; Mulrooney et al. 1992). An analysis of pre-historic and historic residential middens in South Kohala (AD 1400 – 1900) show that in the same region *N. picea*, cowrie species, and *Drupa* species are the most common mollusk taxa (Field 2016), with kūpe'e entering the midden record in relatively small quantities starting in AD 1650 through historic times. The archeological record of kūpe'e utilization for sustenance shows no sign declining resource availability or use through time.

### ***Kūpe'e Connections***

Besides lawai'a, fisher-men and women, it is likely no other group of people know kūpe'e better than those who dance hula. The word 'kūpe'e' refers, perhaps originally, to the animal and its utilization as wrist and ankle hula adornments, and was later adapted to describe the same type of adornments made of greenery. Lei 'ā'ī, or neck lei, can also be made from kūpe'e shells. Their allure comes not only from their visual presence, but also from the light rattling sound made when more than one are set in motion together. Kūpe'e's cryptic nature, which includes nightly emerging and then re-burial, was also used to symbolize hiding or protecting knowledge. Hula hālau (groups) may guard the sacred knowledge of their art through wearing kūpe'e. Because of this spiritual belief and practice, hula dancers are one of the primary

user groups, and many are interested in the biology of this species as well as implementing that information in their harvesting practices.

Another indication of the significance of kūpe‘e is its presence in the Kumulipo, a genealogy chant connecting Hawai‘i’s chiefly lineages with those of the gods and original creation. The Kumulipo begins with the source of life, pō, which comes from the celestial realm, and the first creature called forth, the coral polyp. Of the 2000+ lines of this chant, kūpe‘e appear in the 32<sup>nd</sup> line, along with pipipi (*Nerita picea*) (Beckwith 1951), with which it shares the same genus.

Wearing kūpe‘e as an adornment might also denote status, as will be elaborated on in the final inquiry of this paper. Kūpe‘e found in the Bernice Pauahi Bishop Museum collection included rare colors and patterns, and came from a variety of sources, including the estates of many royal or influential individuals.

### ***Conservation Status***

Kūpe‘e are not listed as threatened or endangered, and no state or federal regulations govern their harvest (State of Hawaii Department of Land and Natural Resources 1941). However, anecdotal information from kūpe‘e harvesters in Hawai‘i suggest a decline in shell size and population density within some historically utilized habitats. It is difficult to confirm this suggestion as size-density data for this species is lacking in Hawai‘i. In addition, as was previously noted, the size range for kūpe‘e is known to have a maximum of about 40mm, and at other locations, such as Kiribati, adults regularly attain such a length, ranging from 20 – 40mm, with a mean of 23.3 mm (F. R. Thomas 2001).

Reason for examination exists, as data supporting modern examples of both declines as well as stability in both the abundance and sizes of fish have been reported from archaeological

studies in other islands in Polynesia (Field, Lipphardt, and Kirch 2016). Shifts in foraging strategies between marine species, as well as development of terrestrial agriculture patterns of resource utilization, are thought to effect resource continuity (Kirch 1982; Field, Lipphardt, and Kirch 2016). Many factors influence adult size and density, including diet, predation, competition, reproductive success, mobility, recruitment, harvesting and other human induced stressors (Riera et al. 2016), such as habitat degradation, and sound and light pollution. No data currently exist describing the relationship between human stressors and kūpeʻe populations. The establishment of baseline population demographic data that will enable future analyses of the extent of population change is an aim of this investigation.

### ***The Kūpeʻe Market***

Commercial harvest of a mollusc species has been shown to substantially intensify the harvesting pressure on that species, and can put it at risk for local extinction (F. R. Thomas 2001). The two main uses for kūpeʻe in Hawaiʻi are food and adornment. Kūpeʻe are not a notable item in the food market, however, shells sold for adornment are easily found in stores and through online retailers based in Hawaiʻi. The price for a shell increases with its length. An 18 mm shell might sell for \$30, while a 21 mm shell sells for \$45. A necklace and bracelet set containing 70 shells 20 to 22 mm in length fetches a price of \$450. Four to five hundred dollars is not uncommon for a modern lei kūpeʻe (Etsy.com 2017).

### **Study Objectives and Rationales**

Despite the cultural importance of kūpeʻe and the plethora of intertidal survey data in Hawaiʻi, none of the published datasets include kūpeʻe life history characteristics, demography, or current and historical use. This is because most surveys are conducted during the day when kūpeʻe are submerged, at night during tides too high for kūpeʻe to emerge, or in unsuitable

habitat (Cox et al. 2013). In general, this species is similar to many other neritids whose life history characteristics are not well known (Giovas et al. 2013).

The objective of this study is to address portions of the knowledge gap related to kūpe‘e reproductive ecology, population dynamics, and historical preferential use. Specifically, I will undertake an investigation with two parts, with cultural context provided by a third part:

1. Long-term histology: To identify gamete developmental stages; determine temporal variations in gamete production; the minimum size at maturity; and the male to female ratio at two locations over the course of a year.
2. Short-term population dynamics: To document population density and size structure, as well as species assemblage and substrate preference at two locations from November 2015 to May 2016.
3. Review of the traditional and historic kūpe‘e collection at the Bishop Museum (Honolulu, HI), coupled with modern usage to provide temporal context on the use of kūpe‘e as bodily adornment.

## **Study Sites**

The Hawaiian archipelago is located in the tropics of the North Pacific, and consists of eight major inhabited islands, as well as numerous atolls, islets and seamounts, between the Island of Hawai‘i in the south and Kure Atoll in the north. The full range of the archipelago spans about 1500 miles, from 18N to 28N and, 154W to 178W. Predominantly northeast trade winds create wetter north and east (windward) coasts, while western and southern (leeward) coasts tend to be dryer, receiving less precipitation. Two major seasons prevail: kau or kau wela, meaning dry season (May - September), and ho‘oilō or wet season (October - April). Rainfall is heavily influenced by Hawai‘i’s terrain. Hawai‘i’s topography ranges from sea level to 4,205 m.

Locally, rainfall can vary from less than 25 cm per year in leeward areas to over 750 cm per year in higher elevations, and windward locales. The length of day and temperature are relatively uniform throughout the year. Daylight varies from 13 ½ hrs to 11 hrs annually, and air temperature generally ranges in the 21 to 32 °C (USGS Pacific Islands Water Science Center 2013)

I have established two study sites on the Island of Hawai‘i (19.5N, 155W) to capture the highly dynamic climatic range of potential kūpe‘e habitat. One is windward Waiuli, the other is leeward Kawaihae (Figure 1). Potential habitat is



Figure 1. Study sites at Waiuli and Kawaihae on the Island of Hawai‘i.

assessed as having rubble to boulders with sand base, ranging from the low tide mark inland as far as boulder/rubble surfaces remain moist.

### ***Kawaihae***

The Kawaihae site is situated within the district of South Kohala, at the base of the Kohala Mountains. It is adjacent to the Kawaihae Boat Ramp, which is easily accessible by vehicle and on foot. The sandy beach that separates the ramp and study site is a popular recreational and fishing area. Kawaihae is known to be hot and dry, with sea surface temperatures ranging from 25 to 27 °C, and receiving under 0.25 m of rain annually (USGS Pacific Islands Water Science Center 2013). At Kawaihae, kūpe‘e habitat consists primarily of basalt boulders, with sand and small rubble at rock bases. It receives a substantial amount of wave energy during ho‘oilō (the wet season), arriving from the north and west, rearranging sand and boulder locations. The habitat extends in a 3 to 4 m wide band approximately 30 m along the



length of the shore. A dense thicket of kiawe trees (*Prosopis pallida*) begins just above the high tide line.

### ***Waiuli***

The Waiuli site lies within Richardson's Ocean Park, which is towards the eastern-most end of the county road running through Keaukaha. This is also a popular recreational area, consisting of a rocky shoreline with intermittent tide pools on basalt rock benches and short stretches of black sand. The study site is broader, with a shallow basalt rubble flat extending seaward along a portion of the shore which becomes exposed at low tides. It also receives lower wave energy due to a protective rock outcropping that disperses wave energies. The habitat here is generally medium sized basalt rubble in sand, extending in a band approximately 10 m wide along 50 m of shoreline. This site also receives considerably more rainfall, averaging more than 3.3m annually, and is situated within a region known for its subterranean freshwater springs, likely contributing to its cooler coastal water temperatures, which range from 21 to 24 °C (USGS Pacific Islands Water Science Center 2013).

## Chapter 1: Histology

### ***Background***

### ***Reproductive Ecology***

Kūpe'e is a marine gastropod mollusc from the subclass Neritimorpha. Neritomorphs are gonochoristic, having distinct male and female sexes, both of which have a single gonad located post-torsionally to the right. The gonad discharges by way of a glandular, pallial, genital duct running parallel with the rectum (Fretter 1984). Females have internal fertilization and produce egg capsules via more elaborate genital ducts. The pallial section of the oviduct has multiple structures to produce and outfit egg capsules. These elaborate structures include albumen, distal jelly, or capsule glands, as well as sperm pouches (bursa copulatrix, receptaculum seminis) (Fretter 1984). In males, the testicular duct is typically long, running superficially along the columellar side of the visceral mass (Fretter 1984).

It is not uncommon for gastropods to exhibit different traits based on gender. Sexual dimorphism may be expressed in shell size, tissue color and radula. Smaller shell size in males has been documented for a number of species (Fretter 1984; Voltzow 1994), most relevant to this study are different shell sizes at reproductive maturity.

### ***Mating***

In the tropics, many invertebrates mate throughout the year (Fretter 1984). Mating occurs on their feeding grounds, which may also be suitable sites for egg deposition. Consistent with other gastropods, during copulation the male mounts the shell of the female, oriented in the same direction, and slightly to the right side (Fretter 1984). As documented in *Nerita albicilla* and *N. undata*, adult male kūpe'e have a structure to the left of the right cephalic tentacle called a cephalic penis, which enlarges during copulation and functions to enter the female's mantle cavity near the vaginal opening and push through a spermatophore "transfer tube" (Iriki 1963).

The cephalic penis can serve to non-invasively identify males if the animal relaxes out of its shell.

### ***Spermatogenesis***

Four primary spermatogenetic stages are displayed by molluscs, described here by order of progression: spermatogonia, primary spermatocyte, secondary spermatocyte, and spermatids or spermatozoa (Horn, Achaval, and Zancan 2005). Spermatogonia, and primary and secondary spermatocytes are immature cells, while spermatozoa are considered mature. The various forms are distinguished by their shape, components, and increasing distance from germinal epithelia. For these analyses, individuals are considered mature if spermatozoa have a head, a rod-like, condensed nucleus, and a long tail. Histological analysis is not able to distinguish between spermatogenetic forms, rather it will be used to differentiate between macro processes of the gonad, including four categories: immature gonad, mature gonad with immature spermatozoa, mature gonad with mature spermatozoa (active gametogenesis), and mature but degenerating gonad.

### ***Oocytogenesis***

The development of oocytes, or oocytogenesis, occurs in female *N. plicata* in four distinct stages (Lasiak and Van der Horst 1988). They are identified by the dominance of (1) (immature) pre-vitellogenic oocytes containing a dense nucleus, with minimal yolk proteins and lipids; (2) (mature) vitellogenic oocytes which house a fully developed nucleus, and protein and lipid filled yolk; (3) degenerating oocytes (immature oocytes and few or no mature oocytes) and cytolysis (oocyte breakdown and reabsorption); and (4) connective tissue and pre-vitellogenic oocytes. It is expected that histological analysis of kūpe'e in this study will be able to identify similar stages as identified above.

### ***Temporal Gonad Development***

There appears to be a degree of variability in gonad development across the genus, with *Nerita yoldii* in Hong Kong undergoing active gametogenesis from March to August, spawning from April to August, and recruiting out on the shoreline from June to December (Yeung 2006). In *Nerita albicilla*, major gametogenetic activity takes place from February to August, spawning from June to October, and recruitment from September to December (Yeung 2006). *Nerita plicata* showed active gametogenesis and continuous breeding potential through the majority of the year, as well as major gametogenetic activity and post-spawning stages from March through September (Lasiak and Van der Horst 1988). There is currently no documentation of kūpe'e gonad development.

### ***Spawning***

In some gastropods, gonad maturation occurs far in advance of spawning events, in others it occurs almost simultaneously (Fretter 1984). *Nerita atramentosa* has no real resting phase, although spawning is mainly a summer event (Scott and Kenny 1998). Immature oocytes are present throughout the year, while accumulation and storage of mature oocytes take place over a six-month period. Similar patterns were recorded for the intertidal limpet *Cellana ornata* in New Zealand (Dunmore and Schiel 2000). Additional spawning patterns for *Nerita* were mentioned in the sections above. Fretter (1984) noted that spawning typically occurs at night and may be influenced by both external and internal triggers. External triggers may include a combination of factors: temperature, light, weather, and lunar and tidal cycles. In *Littorina* species, spring tides associated with lunar or bi-lunar rhythms trigger the release of egg capsules (Fretter 1984).

### ***Ecology of Egg Laying***

It is common for female gastropods to release multiple masses of spawn each season (Fretter 1984). Almost all caenogastropods fix spawn masses to a firm, sheltered substrate that will remain permanent for the embryonic gestation period (Fretter 1984). The length of gestation varies considerably, even between closely related species, and no information exists describing gestation periods for kūpe'e. "A high proportion of marine gastropods in southeastern Australia deposit egg masses beneath boulders in shallow pools where they are shielded from UVR, desiccation, and other environmental extremes" (Przeslawski and Davis 2007). Egg laying in kūpe'e remains undocumented.

### ***Methods***

Ten kūpe'e were collected from each site at the lowest nocturnal tides corresponding with new and full moons once a month for a year. Animals were fixed in 10% formaldehyde for 24 to 48 hrs, then transferred to 70% denatured Histo-prep ethanol. The posterior section of the visceral mass (containing the gonad) was embedded in paraffin and sectioned at 7 to 10  $\mu$ m. Sections were stained according to Humason's Animal Tissue Techniques (Presnell and Schreibman 1997) with hematoxylin and counterstained with eosin Y/ phloxine. Five sections from the center of the gonad were examined using a microscope with an ocular micrometer in the eyepiece. Gonad developmental state was recorded at five random intervals per slide. Females were classified as having a mature (well developed) or immature (poorly developed) macro-gonad structure, and for individuals with mature macro-gonads, either mature (vitellogenic) or immature (pre-vitellogenic and maturing) oocytes present, based on the presence of fundamental components: nucleus, and formulated yolk including a build-up of lipids and proteins. Male specimens were considered mature if spermatozoa had a head, a rod-like, condensed nucleus, and a long tail.

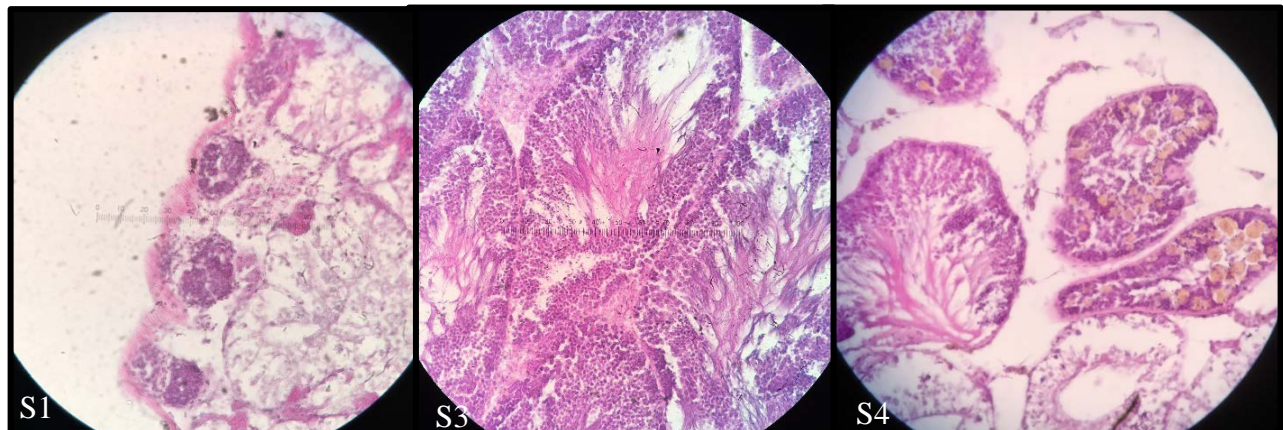


Figure 2. Male Reproductive Stages. Three of the four common stages were documented. S1: Immature or developing gonad, contains pre-spermatozoa. S2: Not documented in this study – inactive but mature gonad, containing fully formed, but empty gonads. S3: All stages and spermatozoa. S4: Spermatozoa degeneration and cytolysis. Magnification 40x.

## ***Results***

### ***Developmental Stages***

Histological analysis identified developmental stages for both male and female kūpe'e.

Gametogenesis in both males and females is found to be characterized by a protracted period of gonad gametogenesis, including immature and mature gametes for the majority of the year, with a short period of degeneration in the fall.

Three developmental stages were found in males (Figure 2): Stage 1: Immature spermatozoa dominate in immature macro-gonad. Stage 2) Gonad is mature but inactive, containing immature spermatozoa within a fully formed macro-gonad. Stage 2 was not recorded during this study. Stage 3) Gonad dominated by mature spermatozoa, in full gametogenesis, with macro-gonad build up; this protracted activity extends from January through September. Stage 4) Cytolysis and macro-gonad degeneration, with immature spermatozoa throughout, from October through December. No periods of gonad inactivity were seen.

Females experienced four developmental stages (Figure 3). Stage 1) Immature (pre-vitellogenic) oocytes coupled with inter-connective tissue dominant. Stage 2) Pre-vitellogenic oocytes dominant, with few vitellogenic oocytes within a fully developed macro-gonad structure.

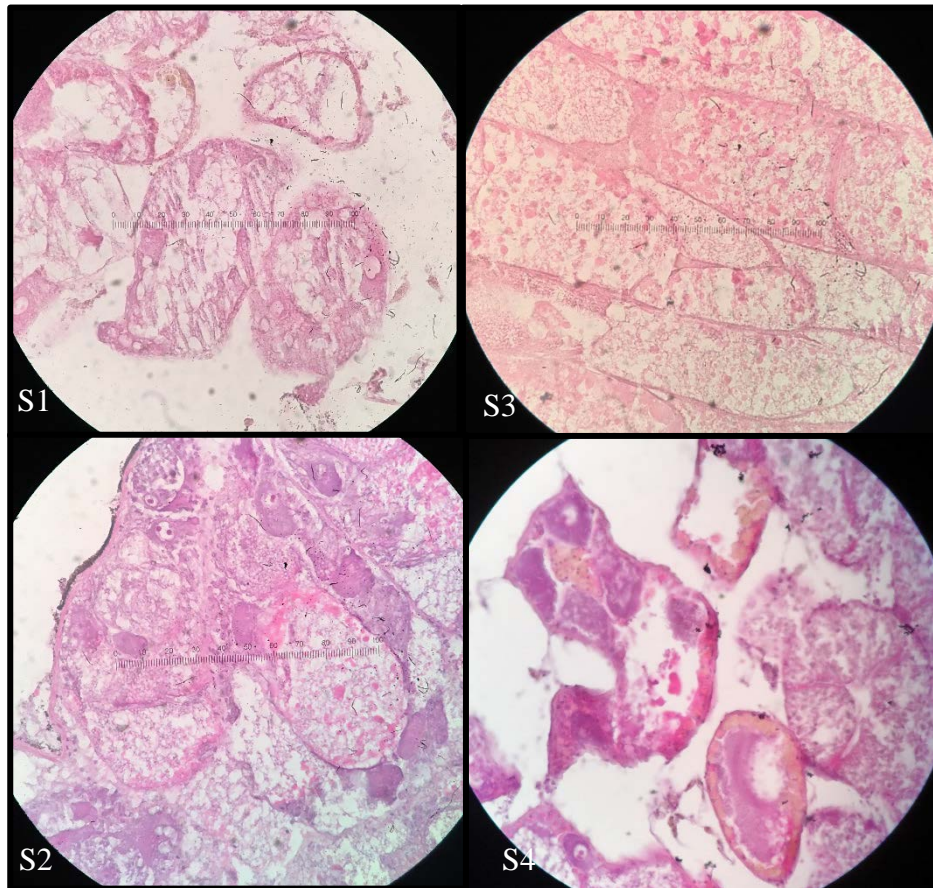


Figure 3. Female Reproductive Stages. S1: few pre-vitellogenic oocytes with connective tissue. S2: Pre-vitellogenic oocytes dominate. S3: Vitellogenic Oocytes with large yolk dominate. S4: Interstitial space, pre-vitellogenic oocytes, and cytotis. Magnification 40x.

Stage 3) A protracted period from December through August when vitellogenic (mature) oocytes with large yolk dominant. Stage 4) Oocyte degeneration, cytotis and few pre-vitellogenic oocytes, occurring from September through November. The mean maximum vitellogenic oocyte length was  $25.08 \mu\text{m}$  ( $n=70$ ), with a minimum of  $16 \mu\text{m}$  and maximum of  $40 \mu\text{m}$ . A regression analysis showed no significant relationship between female shell length and maximum oocyte length ( $F=0.16$ ,  $p=0.692$ ,  $R\text{-sq}(\text{adj}) = 0.00\%$ ).

### ***Shell Length at Maturity***

Across both sites, immature individuals were found up to 13.60 mm shell length, mature females ranged in shell length from 13.00 mm to 22.25 mm, and mature males ranged from

11.50 mm to 22.50 mm (Figure 4, Table 1). A two-sample T-Test found no significant difference in mean shell length between males and females ( $T=1.40$ ,  $p=0.164$ ). However it carries a low statistical power (21 %), so results should be interpreted cautiously. Mann-Whitney Tests found no significant difference in shell lengths between sites for males ( $p=0.1958$  adjusted for ties), or females ( $p=0.8948$ ).

### ***Sex Ratio***

The ratio of females to males is 1.19:1 (147 samples) using data from both sites. Kawaihae had a higher ratio of males (1.31:1) and Waiuli had a higher ratio of females (1.75:1).

### ***Discussion***

#### ***Maturity by Shell Length***

This is the first documentation of kūpe'e shell length at reproductive maturity. It allows for the development of guidelines for a minimum length at reproductive maturity. The majority of individuals will be mature at shell lengths greater than 14 mm (obtained by rounding

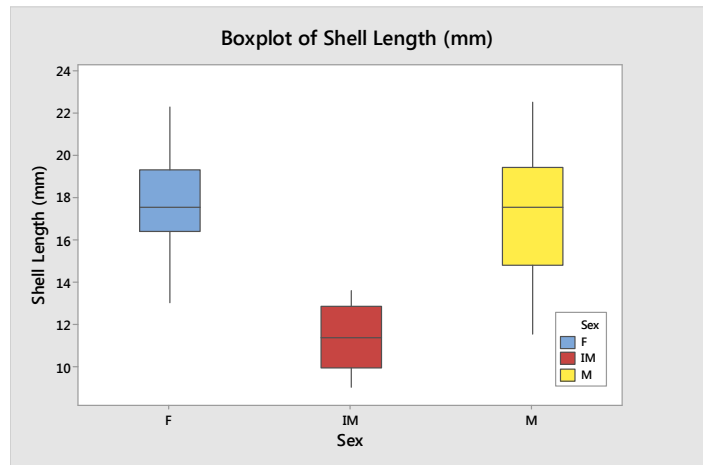


Figure 4. Boxplot of shell lengths for sites combined: females, males, and immature individuals.

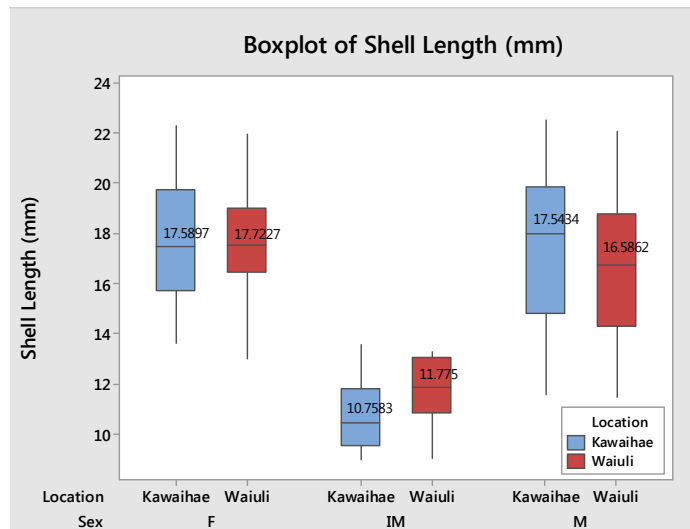


Figure 5. Boxplot comparison of Kawaihae and Waiuli populations: females, males and immature individuals.

	MINIMUM (mm)	MAXIMUM (mm)
<b>FEMALE</b>	13.00	22.25
<b>MALE</b>	11.50	22.50
<b>IMMATURE</b>		13.60

Table 1. Shell length ranges for female, male and immature individuals.



13.6 mm up to the nearest integer for ease of general utilization), which establishes a minimum length under which individuals should not be harvested.

Contrary to many gastropods, kūpe'e showed no sexual dimorphism; both sexes display a variety of shell color and pattern, and there is no significant difference in shell length. There is also no evidence of an uneven ratio of females to males. Because no significant difference was found between male and female shell lengths, the minimum length of 14 mm for harvest applies to mature individuals of both sexes.

### ***Reproductive Stages***

Male individuals were found to have three distinct stages (1) Immature, (3) Mature gonad and spermatozoa, under gametogenesis, and (4) Mature but post-spawning/degenerating gonads. Stage (2) Pre-spermatozoan (common to this genus), or regenerative stage might be sufficiently short to remain undocumented by this study. Females displayed four distinct stages, identified by the dominance of (1) Pre-vitellogenic oocytes, (2) Vitellogenic oocytes, (3) Degenerating oocytes and cytolysis, (4) Interconnective tissue and pre-vitellogenic oocytes. Immature individuals of both sexes were identified by having minimal macro-gonad structure, with immature gametes.

### ***Egg Length***

Egg length appeared to vary with reproductive stage, increasing with increasing oocyte generation. An egg in S2 will have a smaller length than those in S3. Oocytes in S3 are also larger than in post-spawning S4. However, caution must be taken in using a 2D cross-section measurement of a 3D object because its measurement is subject to the particular angle of sectioning. For example, a large oocyte could be oriented at its narrowed margin, resulting in an inaccurate measurement. In an effort to reduce this unequal orientation, multiple measurements of maximum oocyte length were taken from histologic sections in each individual.

### ***Spermatophore Transfer Tube***

As was noted by Iriki (1963) in *N. albicilla*, kūpe‘e also utilize a cylindrical spermatophore transfer tube, about 4 mm in length, with a rounded head at one end and a thin “tag” at the other, extending an additional 2 mm. The spermatophore transfer tube is conducted by the cephalic penis during mating, and deposited internally in the female. Use of a spermatophore transfer tube is quite common in nerites, however, this is the first such documentation for kūpe‘e.



Figure 6.  
Spermatophore  
transfer tubes.

### ***Timing of Gametogenesis***

The results of this histological analysis suggest kūpe‘e are capable of breeding for the majority of the year. Females undergo active gametogenesis from December through August, with post-spawned individuals appearing from September to November. Males display similar pattern: undergoing active gametogenesis from January through September, with a period of post-spawning degeneration from October through December.

Developmental Stage		Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
FEMALES	Gametogenesis												
	Post Spawning/Degeneration												
MALES	Gametogenesis												
	Post Spawning/Degeneration												

Table 2. Timing of gonad development.

### ***Fecundity***

Within the range of shell lengths measured in the histological portion of this study (maximum = 22.50 mm) there appears to be no maximum shell length at which gonads “shut off”. All mature individuals, both male and female, had active gonads. Oocytes had a maximum length of 40  $\mu$ m, and unfortunately unequal histological sectioning prevent this study from comparing the oocyte count of larger females to smaller females, but it was observed that, in

general, larger individuals also had larger sections of macro-gonads (thicker swaths of gonad across consecutive slides). In many species, female size is directly related to oocyte production, with larger females producing more oocytes (Harding, Mann, and Kilduff 2007). Future studies utilizing equivalent histological orientations could be used to better evaluate kūpe'e fecundity.

### *Caviats*

This study did not directly measure the ratio of gonad to body mass to generate a Gonad Index by weight, due to the very small weight of the reproductive organs and their attachment to the gut. Separation of the gonad from the gut for measurement could not be done with reasonable confidence. However, future studies establishing a gonad index for kūpe'e would be useful for management purposes.

Part of the impetus for this thesis investigation was to better understand population sizes and guidelines for a sustainable harvest. In the absence of density data (now obtained through this study), coupled with the destructive nature of histology, it was deemed wise to be cautious of causing harvesting impacts. Therefore, monthly collection was limited to 10 individuals, in expectation that perhaps 5 of the 10 would be females, able to provide oocyte data. Because of this limited sample size, these results are subject statistical errors in which a finding of no significance is falsely accepted and an underlying significant effect is missed.

### ***Annual variability in gonad production***

There is a need for annual data collection in intertidal species, which have been shown to experience significant variability in gonad production across annual reproductive seasons (Dunmore and Schiel 2000). Future studies are necessary to better understand whether the results of this study period are representative of long-term trends in gametogenesis, and in turn, potential spawning and shoreline recruitment.

## Chapter 2: Demographics

### *Methods*

Within the low intertidal range, inner and outer transects through kūpeʻe habitat were identified. Transects were approximately 1 m apart, and 1 m<sup>2</sup> quadrats were deployed every other meter to record kūpeʻe abundance, shell length, composition of the benthos, and invertebrate assemblage.

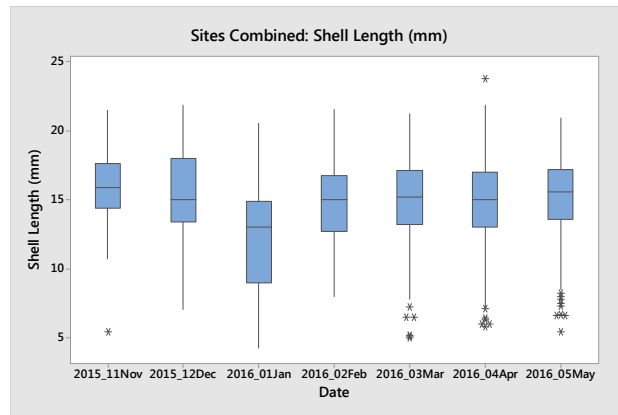


Figure 7. Boxplots and means of monthly shell lengths.

### *Results*

For the period between November 2015 and May 2016 across both sites, 1036 individuals were sampled. The mean shell length was 14.90 mm, minimum = 4.30 mm, maximum = 23.70 mm. The inter quartile range is 13.30 – 17.00 mm. Mating was seen throughout the study period (Figure 7).

A Kruskal-Wallis Test found that with sites combined, shell length varied significantly by month ( $p < 0.001$ ,  $H = 44.84$   $DF = 6$ ). The months with the biggest differences were January (mean= 13.0 mm) and November (mean = 15.9 mm).

## Results at Individual Sites

	<b>SHELL LENGTH (mm)</b>						
	<b>NOVEMBER</b>	<b>DECEMBER</b>	<b>JANUARY</b>	<b>FEBRUARY</b>	<b>MARCH</b>	<b>APRIL</b>	<b>MAY</b>
<b>KAWAIHAE</b>							
Mean		15.2	12.2	14.4	14.9	14.7	13.7
Minimum		7.1	4.3	8	5	5.8	5.5
Maximum		21.8	20.5	21.5	21.2	23.7	20.4
<b>WAIULI</b>							
Mean	16	16.1		15.47	15	14.7	16
Minimum	10.75	5.4		6.5	6.3	8.2	5.4
Maximum	21	21.45		20.4	20.5	19	20.9

Table 3. Descriptive analysis of shell lengths by month.

At Kawaihae, shell lengths ranged from 4.30 mm to 23.70 mm, with a mean of 14.32 mm, and at Waiuli, shell lengths ranged from 5.40 mm to 21.45 mm, with a mean of 15.52 mm (Table 3). A two-sample T-Test found the means between sites to be significantly different ( $p=0.000$ ,  $T=-6.01$ ).

### Shoreline Recruitment

The smallest individuals (4 – 10 mm range) are present at both sites throughout the study period.

Kawaihae displayed small individuals each month, with an influx in January, March, April and May (Figure 8). The smallest individual was recorded in January (4.30 mm).

Waiuli experienced an influx of smaller individuals in March, April, and May (Figure 9). However, the lower size ranges are present each month and the smallest individual recorded was in December (5.30 mm).

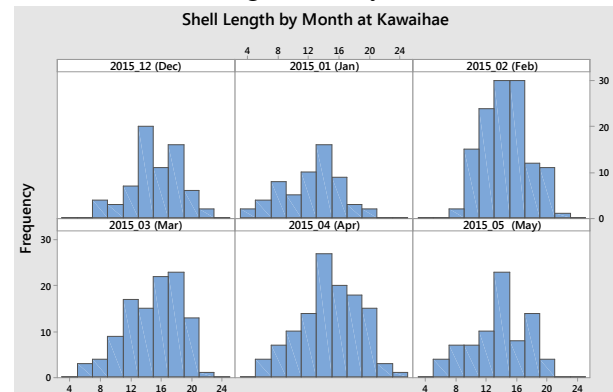


Figure 8. Monthly shell length at Kawaihae.

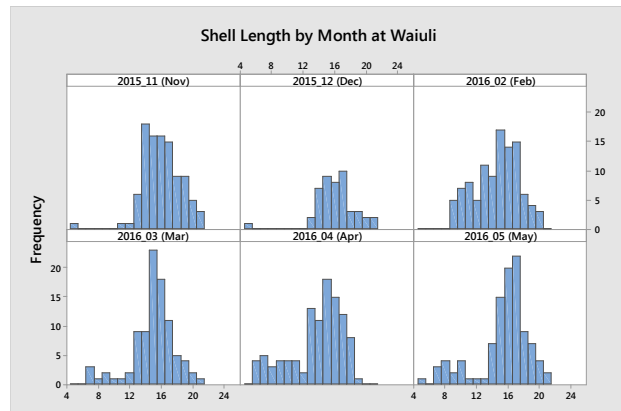


Figure 9. Monthly shell length at Waiuli. The smallest individuals are found March through May.

### ***Habitat***

The preferred benthic cover for kūpe'e active periods is basalt rock (greater than 0.1 m<sup>2</sup>, 50% frequency), basalt rubble (less than 0.1 m<sup>2</sup>) occurred 22% of the time, followed by mixed coral and basalt rubble at 12%, sand at 11%, coral rubble 3%, and coral (greater than 0.1 m<sup>2</sup>) macroalgae, grass, microalgae, and cement occurring at a frequency of less than 1%.

The most common invertebrate found was *N. picea* at a frequency of 86%, followed by crabs (4%), *Morula granulata* (3%), *Peronia verruculata* (3%), and *Littoraria* species (2%). The following species occurred less than 1% of the time; *Smaragdinella calyculata*, miscellaneous hermit crabs, *Isognomon californicum*, *Echinometra mathaei*, and *Cellana exarata*.

### ***Densities***

The density at Kawaihae was higher than at Waiuli (15.8 individuals/ m<sup>2</sup>, and 7.9 individuals/ m<sup>2</sup>, respectively) (Table 4). Those familiar with kūpe'e harvesting in Hawai'i say that gathering takes place on or around the new

LOCATION	MEAN SHELL LENGTH (mm)	DENSITY per m <sup>2</sup>
KAWAIHAE	14.32	15.8
WAIULI	15.52	7.9
KANEOHE	17.6	2.1
KIRIBATI	22.3	N/A

Table 4. Comparative shell lengths and densities across sites.

moon, which creates very low tides. In order to test the effects of bright or dark moons on kūpe'e density, an ANOVA was conducted to compare bright and dark sampling nights at Kawaihae and Waiuli, respectively. However, the sample size is small, so the result of no significant difference should be taken cautiously ( $\alpha = 0.05$ ,  $p=0.13$ ,  $F=2.43$ ,  $df=3$ ).

### ***Discussion***

The density at both study sites was higher than recorded in Kane'ohe, HI, by Kawelo (1997, unpublished), which was 2.1 individuals/ m<sup>2</sup>. However, Kane'ohe had higher mean shell length (17.6 mm) than either Kawaihae or Waiuli.

Kaneʻohe, is located on the Island of Oʻahu, which has a population of just under 1 million people on an island of about 1500 km<sup>2</sup>, compared to the Island of Hawaii, which houses a population of 200,000 people on a land mass of ~10,400 km<sup>2</sup> (The United States Census Bureau 2017). Human development and harvesting impacts have a magnified intensity on Oʻahu. The Kaneʻohe study site is located within a large protected bay, which is typically prime kūpeʻe habitat. The lower density in Kaneʻohe may be due to the impacts of coastal development and intensive harvesting pressure from the relatively larger human population.

All locations in Hawaiʻi have smaller mean shell lengths than were recorded in Kiribati, which was 22.3 mm (F. R. Thomas 2001), however, Kaneʻohe had the largest mean shell lengths of the three Hawaiʻi sites. It is possible that larger shell size found in Kiribati can be attributed in part to the comparatively much lower human population in Kiribati (~110,000 people spread over 33 atolls) (The World Bank 2017) and much the more extensive nearshore lagoon habitats of the atolls, coupled with mostly incidental harvesting (a diverse selection of mollusc are harvested, and kūpeʻe are not the most commonly targeted species).

***Densities of Bright vs. Dark Nights***

*He pō hīhīwai.*

*A night for the hīhīwai.*

*A gainful night. The hīhīwai are freshwater shellfish. On starry nights, they climb upon the rocks where they can be seen and gathered.*

– ‘Ōlelo No ‘eau 903

This ‘ōlelo no ‘eau speaks to the connection ka poʻe kahiko (meaning “the people of old”) have observed between hīhīwai (*Neritina granosa* Sowerby, 1825) and dark nights – because

nights are most starry when the light of the moon does not block them out. The observational knowledge captured in this saying provides the bases for investigations into the connection in to kūpe'e light sensitivity. An additional parallel between Hawaiian and Western science exists in that hīhīwai and kūpe'e are closely related in both Hawaiian epistemology and current phylogenetic theory. Until recently hīhīwai were classified in the genus *Nerita*, and although they now reside in a separate genus, they remain in the same family, Neritidae.

The finding, in this study, of no significant difference between bright (around the full) and dark (around the new) moons should be interpreted cautiously as the sample size was very small. Kawelo monitored densities along Kane'ohe Bay, and found higher densities during dark nights, ranging from 1.5 – 4.75 kūpe'e/ m<sup>2</sup> as compared to 1.3 – 1.7 kūpe'e/ m<sup>2</sup> during bright nights (statistical significance unknown). This question of light effecting foraging and reproductive behaviors may have broader implications for coastal development if it is found that increased ambient light correlates to decreased densities.

### ***Shoreline Recruitment***

Kawaihae and Waiuli populations showed significant shell length variability by month, especially between November, with the highest mean shell length, and January, with the lowest. This information, coupled with the results of the histological study, which showed active production of mature gametes from January through August, followed by post-spawning gonad degeneration from September through December, suggests that, while spawning may occur throughout the year, a significant spawning and gonad transitional period takes place in the Fall. Recruits (4 – 10 mm) were found at both sites throughout the study period, indicating that the degeneration and resting phase does not significantly affect shoreline recruitment.



Again, recruitment patterns often occur with annual variation, so these findings would need to be compared with long term monitoring to clarify the timing of events and the intensity of recruitment (i.e. do these results represent a “high”, “normal” or “low” recruitment, and is recruitment changing over time).

## **Chapter 3: Traditional and Historic Adornment: the Bishop Museum Collection**

### ***Background***

Many forms of guidance exist to interpret the values of a particular culture. One way is to examine things specified by name. The general word for a shelled animal in Hawaiian is pūpū, and certain groups of shelled animals, such as kūpe‘e, were specifically named. In fact, many specific names for kūpe‘e exist, based on their color and pattern. According to Titcomb et al. (1978), kūpe‘e ula (red) were red; anuenue (rainbow) were red or black striped; palaoa (whale tooth ivory) were creamy white; ‘ele‘ele (black, dark) were black; kani‘o (vertical stripes) were black with white streaks; mahiole (warrior’s helmet) were white with red stripes; and puna were rare (no color description). The rarest and most precious kūpe‘e were saved for ali‘i (royalty) (Pukui 1986). Such is the case of the kūpe‘e, which were gifted to Queen Kapi‘olani as she traveled across Hawai‘i, and were eventually made into a spectacular lei now on display at the Bernice Pauahi Bishop Museum (BPBM).

### ***Methods***

Kūpe‘e used for bodily adornment within the collection at the BPBM Ethnology Department were included in this study. The Museum’s acquisition records for each piece were obtained. Random shells from each piece were measured, and notes on their adornment type, shell length, cordage material, the incorporation of other natural materials, and any shell processing were documented.

### ***Results***

The BPBM houses many kūpe‘e pieces with unknown acquisition dates. However, those acquisitions with known dates, range from “before 1889” through 1932, although it is likely some are more recent based on more modern cordage materials. The pieces come from many

sources, including the Queen Lili‘uokalani Collection, the Kapi‘olani-Kalaniana‘ole Collection, the Ke‘elikōlani Collection, the J.S. Emerson Collection, and the Lucy Kaopaulu Peabody, Edgar and Kalani Henriques Collection. These names may be familiar to many readers as belonging to ali‘i (royalty) lineages. Even the pieces that are from the collections of individuals connected to a specific period in time, do not reliably have information on shell harvesting locations or dates.



Figure 10. Bracelet of mahi‘ole shells strung on deteriorating silk ribbon.

However, these collections are interesting based on the lengths of shells used (indicating a degree of shell length desirability); the diversity of colors and patterns; the types of processing done to shells; the varieties of materials used to string shells; as well as the incorporation of other species in the pieces.

### ***Qualitative Analysis***

Shells were made into necklaces, chokers, and bracelets. The collection included pieces in a range of states – from individual shells without indication of a previous incorporation into a broader bracelet, necklace, etc., to sets of shells along with the deteriorated material that was used to hold them together (Figure 10), to fully intact, well preserved pieces and matched sets.

### ***Colors and Patterns***

Shells in the collection displayed many colors and patterns. In addition to a base color, most shells had checkered/chevron patterns, spots, and/or stripes. The collection included shells of many base



Figure 11. Anuenue color variation with red and black stripes on white.

colors, including white, black, grey, yellow, orange, pink, and red. There are kani‘o, which are black with vertical white streaks; anuenue, with alternating red, black and white stripes, and mahi‘ole, white with red stripes (Titcomb et al. 1978).

### ***Matching Shell Sizes***

Several pieces show incredible accuracy in matching shell lengths – containing consecutive identically sized shells – within a tenth of a millimeter.

### ***Material Used for Stringing***

Although museum records do not indicate whether the material

currently connecting the shells is original, several material types remaining were frequently used: silk ribbon, olonā (*Touchardia latifolia*), and other unknown natural fiber. One piece belonging to the Queen Liliuokalani Collection used copper wire, bending it to the shape of each shell (Figure 13).

### ***Used in combination with other invertebrates***



Figure 12. *N. exuvia* coupled with kūpe‘e ‘ele‘ele.



Figure 13. Copper wire strung bracelet.

Many pieces included other invertebrates, some of which closely resemble kūpe'e. One piece includes a shell of *Nerita exuvia* Linnaeus, 1758 (Figure 12), which has a central Indo-West Pacific distribution, including Indonesia and the Philippines (Frey 2014).



Figure 14. Kūpe'e palaoa strung with palaoa (whale tooth).

### ***Shell Processing.***

Some shells showed signs of post-processing. The Queen Lili'uokalani collection included two pieces, which appeared to be sanded to imitate kani'o, the white stripe pattern



Figure 15. Black shells sanded to give the appearance of white kani'o stripes.

(Figure 15). Another piece was coated with an orange-red lacquer, which was seen chipping off at the edges (Figure 16).



Figure 16. This modern piece incorporates both another invertebrate (*Turbo petholatus* Linnaeus, 1758), as well as a colored finish, which is seen here chipping off.





Figure 17. Queen Kapi'olani's lei kūpe'e, containing the largest recorded shell at 42mm. Of all the pieces, one lei that distinctly stands out includes a ring of palaoa (sperm whale tooth), and is paired with palaoa, or white, kūpe'e (Figure 14). Whale palaoa is highly prized and was fashioned into a variety of adornments, the most incredible of which is the lei niho palaoa, which is "a hook-shaped ornament made originally from a sperm-whale tooth (palaoa or palaowa) and suspended by two coils of braided human hair." (Buck 1959). Palaoa were also fashioned into more modern hooks, beads for necklaces, as well as carved into detailed imitations of kūpe'e, called kūpe'e palaoa (Pukui 1986). Palaoa adornment denoted the high status of its wearer. Here, palaoa colored kūpe'e are fashioned with whale palaoa, perhaps indicating the significance carried by these kūpe'e.

Perhaps the most well preserved and diverse piece belonged to Queen Kapi'olani, wife of King Kalākaua (Figure 17). This incredible piece displays almost every kūpe'e color and pattern type, some that are not described, as well as shells other than kūpe'e. It is said that the Queen was gifted individual shells by maka'āinana (common people) during her travels around the Hawaiian archipelago. They were later combined into this incredible lei.

### ***Quantitative Analysis***

Measurements of 208 kūpe'e were taken from the BPBM collection. The mean shell length is 21.7 mm, median 21.8 mm. Minimum shell length is 13.5 mm and maximum is 42.0

mm. The mean length of kūpe‘e recorded in this study is 14.90 mm, compared to 21.7 mm, the mean shell length from the BPBM collection. A two-sample T-Test comparing mean shell lengths from the BPBM Collection (n=208) and the Hawai‘i Island Sites (combined) (n=981) found a significant difference in means ( $p < 0.001$ , T-Value = 18.77).

#### ***Desirable Shell Population at Bishop Museum Mean (21.7mm)***

Using the mean shell length (21.7 mm) of the BPBM collection as an indicator of desirable shell length for adornment, we find that only 0.3% of all Hawai‘i Island kūpe‘e recorded during this study had were this length or larger.

#### ***Desirable Shell Population at 20mm***

If the desirable shell length is reduced to 20mm (an anecdotal harvesting size), less than 5% of the Hawai‘i Island population fits into this category.

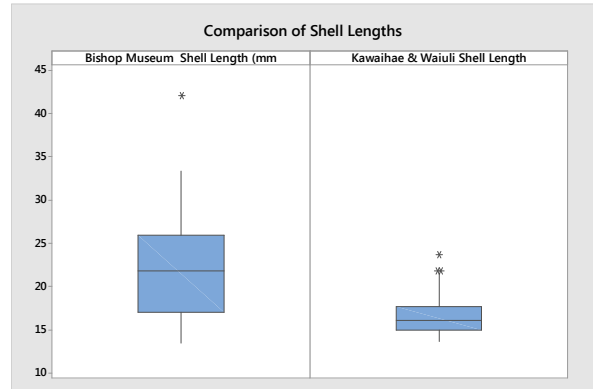


Figure 18. Comparing shell lengths from the BPBM collection and the study sites. The BPBM shells are significantly larger.

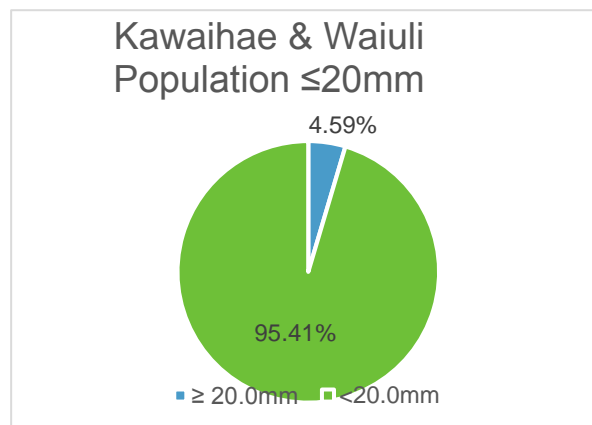
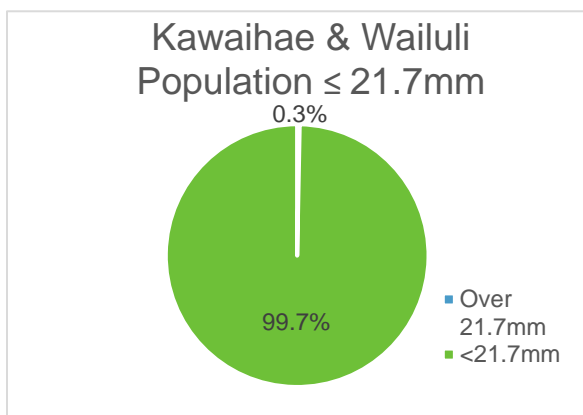


Figure 19. Desirable Shell Length in Shoreline Populations. Less than 1% of the sampled population is equal to or larger than the BPBM mean. Less than 5% of the sampled population is greater than or equal to the anecdotal harvest length of 20mm.

## ***Discussion***

The BPBM collection provides almost a century of insight into the material use of kūpeʻe. Their presence in royal collections, and their connection to palaoa, another highly valued adornment, reaffirms their importance in the Hawaiian cultural view. The collection includes pieces illustrating great skill in shell selection and adaptation through the use of modern materials. Several historical museums in Hawaiʻi house kūpeʻe collections. Further studies of those collections may provide insight to a broader swath of kūpeʻe adornment, and the prevalence of harvesting larger shell sizes.

It is unlikely that the BPBM mean shell length (21.7 mm) would be found as the mean for populations in Hawaiʻi today. It is much more likely that shells such as those in the collection, or those available for commercial sale today, represent the largest individuals in a given population. Targeting the largest individuals can lead to lower mean shell lengths unless sufficient time for replenishment is allowed. Future studies should include those aimed at understanding kūpeʻe growth rate, catch rate, and size structure at a broader set of sites across Hawaiʻi.

## **Conclusions**

### ***Climate Change***

Human induced climate change is a settled fact (Bernstein et al. 2007), the impacts of which are far reaching and particularly concerning in lowland, coastal regions (Lathlean, Seuront, and Ng 2017; C. D. Thomas et al. 2004). Intertidal communities are and will continue to be affected by accelerated sea level rise (SLR), ocean warming, ocean acidification, and increased pollution due to ocean of coastal population centers.

The global average for SLR is 3.1 mm/ year (Williams 2013), however, various scenarios estimate global SLR to increase by 0.3 m to 0.53m by 2050 and 0.75 m to 1.9 m by 2100



(Marrack and O’Grady 2014). SLR is a driving factor in coastal erosion, with rates of sandy beach erosion exacerbated under future scenarios (Zhang, Douglas, and Leatherman 2004). The ability of sandy beach habitat to migrate, and then for the intertidal ecological community, including kūpe‘e, to re-establish within that new habitat will be critical in the future.

Predicted reductions in global wind speeds and shifting ocean currents may impact distribution potential for kūpe‘e, decreasing the ability for remote recruiting sources to reach previously enriched areas, and making locally driven recruitment even more important. As previously noted, the specifics of this species’ larval/planktonic stage are unknown, but it is possible for warming ocean temperatures to affect the seasonal timing, duration, distribution and resiliency of larva. Warmer ocean temperatures have been linked in Hawai‘i to shifts in macro-algae diversity and benthic cover (Cox et al. 2013). Kūpe‘e recruit to micro-algae dominated substrate. Shifts from micro- to macro-algae dominated low-intertidal regions may decrease available food sources as well as provide a physical barrier to kūpe‘e travel from beneath the sand and up onto boulders or limestone substrate for foraging and mating.

### ***Management Strategies***

Potential strategies to promote a sustainable population:

1. Select for sizes above the size at maturity, 14mm, ensuring the population will always contain reproducing individuals. It is encouraging that the mean shell length for both populations are larger than this value.
2. Kūpe‘e have almost continuous breeding potential throughout the year, excluding the fall. Therefore, there is no particular periods of time when kūpe‘e are especially vulnerable to harvesting pressure.

3. Desirable shell lengths (20 – 25 mm) occur at of less than 1% monitored populations. It is likely that harvesting these sizes are removing the largest individuals from the population.
4. Males and females exists in even ratios and similar sizes, so practices of targeting the largest individuals for harvest do not significantly affect a single sex.
5. Kūpe‘e are a relatively sedentary and predictable species, and are easily monitored, so if community members or user groups were interested in understanding localized kūpe‘e populations, including what local abundance and scarcity look like, it would not be very technically difficult. In addition to not being difficult, this type of monitoring would greatly help to inform local harvesting strategies.
6. Kūpe‘e are vulnerable to human caused habitat degradation, such as water pollution, shoreline hardening, and light and noise pollution.
7. Kūpe‘e are vulnerable to climate change impacts such as sea level rise, shifting sand regimes, and increases in macro-algae assemblages. Efforts should be made to model and protect kūpe‘e habitat migration.

### ***Further Studies***

A substantial need exists to have archipelago-wide kūpe‘e population data. In this very brief glimpse into the population dynamics occurring between sites on different islands (Hawai‘i and O‘ahu) it is clear there is potential for large variations to exist. In addition to population data is a need for kūpe‘e predation and harvesting data to understand drivers of population reductions. And if populations are being decreased in predictable ways, such as targeting the largest individuals, there is a need to understand the role of the largest individuals to the broader

population. This touches on fecundity and the role of large females. The people of Hawai‘i have a long history of kūpe‘e use, with no indication in the midden record of a decline in use. What traditional management strategies fostered continued resource abundance through time? How can they inform human interactions today?

Finally, all of these efforts should be placed into the context, not of previous climate trends, but of a future of changing climate. Where and how will kūpe‘e habitat change, and what steps can be taken to ensure those new intertidal habitats are able to sustain life?

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