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LENGTH-WEIGHT RELATIONSHIP OF THE KELP FOREST GASTROPOD AND EMERGING FISHERIES SPECIES, KELLET'S WHELK, *KELLETIA KELLETII*

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ABSTRACT In this study, the length-weight relationship (LWR) was determined for the marine gastropod and commercial fisheries species, Kellet's whelk (*Kelletia kelletii*), and possible site- and sex-based differences in the LWR were assessed. Data were collected from 761 Kellet's whelks (1.6–15.5 cm shell length, 0.51–404 g total weight) that were brought to port by commercial fishermen or collected using SCUBA from three regions across the US geographic distribution of the species: San Diego, Santa Barbara, including the Northern Channel Islands, and Monterey. Model fitting revealed a cubic function to represent the LWR of the entire dataset with strong explanatory power. The fitted model suggested the species demonstrates slightly negative allometric growth, indicating that shell length grows faster than the width of the organism. Whelk sex and collection site did not impact the LWR. The information from this study can be used to inform management decisions for Kellet's whelk conservation, aquaculture, and fisheries harvest and guide future research.

KEY WORDS: Kellet's whelk, *Kelletia kelletii*, length-weight relationship, fisheries, management, California

INTRODUCTION

Kellet's whelk (*Kelletia kelletii*, Forbes, 1850) is a large (up to 17.5 cm), predatory gastropod found primarily in subtidal kelp forests at depths of 2–70 m (Rosenthal 1970). Following a northward range expansion first observed in approximately 1980 (Herrlinger 1981), the current geographic range for the species is in the eastern Pacific Ocean from Monterey, CA, to Isla Asuncion, Baja California, Mexico (Zacherl et al. 2003, CDFW 2020a). Specimens are slow-growing (requiring at least 30 y, on average, to reach near-maximum size), exhibit high site fidelity, and become sexually mature at approximately 6 cm for males and approximately 7 cm for females (Rosenthal 1970, Cumberland 1995, CDFG 2006, White et al. 2022). Reproduction occurs in late spring and summer when adults migrate to shallower waters and form mating aggregations. Eggs are attached to a hard substrate, and hatching occurs after 30–34 days. Larvae are pelagic, facultative lecithotrophs with an approximately 5.5–9 wk larval duration (Romero et al. 2012).

Kellet's whelk is thought to play an important role in kelp forest community dynamics by controlling the abundance of kelp and algal grazers (Halpern et al. 2006). Kellet's whelk is also the focus of a growing fishery in California. Harvest increased drastically from the late 1970s, when recorded landings were nearly nonexistent, to 2006 (CDFG 2006, 2009), and the species currently supports the second largest commercial molluscan fishery in California by landings weight and value (CDFW 2022). Given that several traits of the species make it a likely candidate for overexploitation (CDFG 2009, Clare et al. 2022), the California Department of Fish and Wildlife began regulating the fishery in 2012 in response to this growing take. Harvest is prohibited from mid-March through June 30, a time coinciding with whelk reproduction, and whelks may not be collected in protected areas or within 1,000 ft of the low tide mark. The commercial fishery is limited to a Total Allowable Catch of 100,000 pounds (45,359 kg), measured as the wet weight of organisms (CDFW 2020a). Commercial take is also limited to hand collection and incidental take via lobster or crab traps, with take by crab traps only allowed south of the Monterey-San Luis Obispo County line and take by lobster traps only permitted south of Yankee Point, Monterey County. Recreational harvest requires capture by hand or hook and line, and only 35 organisms can be collected per person per day (CDFW 2020a). Currently, there is no legal size limit for the commercial or recreational fishery.

Despite this increased management focus, several pieces of biological information important to fisheries management are either not well understood or are unknown for the species (CDFW 2020a). For example, the length-weight relationship (LWR) for Kellet's whelk is currently unknown. The LWR is commonly used for guiding fisheries management and marine conservation (Froese 2006, Dikou 2023). Monitoring the LWR of a species may be used to assess biomass and productivity levels of fisheries stocks (Morais & Bellwood 2020) and seasonal effects on these metrics (Ariyanto et al. 2018). The LWR is also a fundamental equation in bio-economic models used to simulate fish population responses (e.g., growth and resilience) to harvest rates and guide sustainable fisheries management and marine conservation strategies (White et al. 2012, Botsford et al. 2019).

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To fill this information gap, the LWR of Kellet's whelk was assessed. Kellet's whelks were collected from three areas in California, measured, and weighed; a subset of individuals was also sexed. In addition to considering the basic form of the LWR, differences in the LWR among populations and between male and female specimens were explored. Differences in LWRs among populations and across time can be used to estimate the impacts of environmental factors (e.g., resource availability, water quality, and temperature) and harvest (fishing effort and fish size) on populations (Froese 2006, Ngor et al. 2018). Within the historical range of the Kellet's whelk, the San Diego coast is typically influenced by the relatively warmer Southern California Eddy, whereas the Santa Barbara region, inclusive of the Northern Channel Islands, experiences both warm and cold temperature regimes (Gosnell et al. 2014). In contrast, the expanded range north of Point Conception is generally influenced by the cold California current (Gosnell et al. 2014), which may impact whelk growth (Rodriguez et al. 2015). Oceanographic differences may also limit population connectivity (gene flow) among these regions and lead to localized changes in the LWR. Accordingly, samples collected in these regions were used to test for a significant effect of the collection site on the LWR of the species. Sex may also influence the LWR, as males may reach sexual maturity at a smaller size and may be under different evolutionary pressures relating to energy investment in gonads and growth (Cumberland 1995).

MATERIALS AND METHODS

Sample Collection

Kellet's whelks were obtained opportunistically for this study from commercial fishermen operating out of the ports of San Diego (including Point Loma, samples purchased February 2011) and Santa Barbara (including the Gaviota coast and Northern Channel Islands, samples purchased October 2010–May 2011) (Fig. 1). More precise geographic information on the collection locations was not provided by the fishermen.

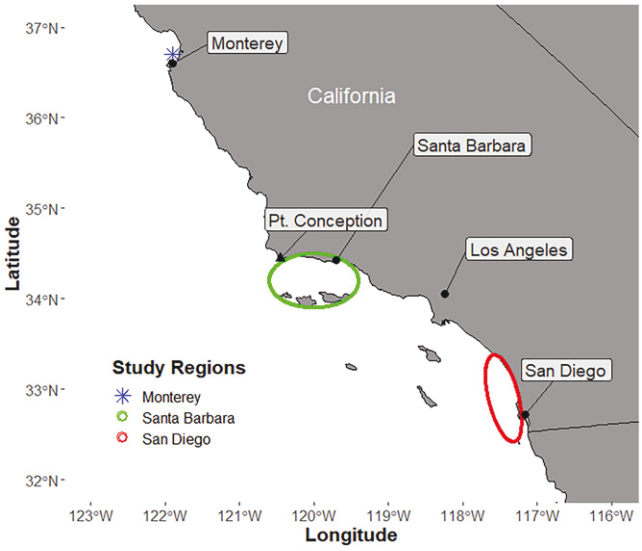

Figure 1. Map of *Kelletia kelletii* collection sites and nearby ports in California, USA. Point Conception, a feature that largely divides biogeographic provinces and water parameters in the state, is also depicted.

Each whelk was measured for maximum total length to the nearest mm from the apex of the shell to the end of the siphonal canal using calipers. The total wet weight (mass, in grams, including shell) of each Kellet's whelk was measured to the nearest one-hundredth of a gram with a top-loading balance. Sex was determined for a subset of the whelks by inspecting specimens for the presence or absence of a penis after shells were cracked with a vise and removed.

These samples did not include smaller-sized Kellet's whelks, as they were not targeted by fishermen and may not be captured via traps. Additional whelks were thus opportunistically collected via SCUBA from a large population of young-of-year and subadult Kellet's whelks near Monterey in July 2017 to more fully characterize the LWR across the complete size range of the species (Fig. 1). Kellet's whelks were collected from the benthos at 13–17 m depth, weighed, measured, and returned to the reef collection sites (CDFW Scientific Collection Permit 8018 to C. W.). Kellet's whelks from Monterey were not sexed due to the difficulty of sexing living individuals, especially those that are small and immature.

Analysis

Cubic models (e.g., $W = aL^b$) are commonly used for describing the relationship between length and weight in marine gastropods and other organisms (Froese 2006, McKinney 2006, Kasapoglu & Duzgunes 2014, Saleky et al. 2016). These models assume the weight of the organism increases proportionally with its length. Visual inspection of the LWR suggested a cubic relationship may be appropriate for Kellet's whelk. For comparison, both cubic and linear models were fit to the data and compared using the AIC (Al Nahdi et al. 2016).

Given the selection of the cubic model for representing the LWR, length and weight were log-transformed to allow the impact of site and sex on the LWR to be evaluated. Transforming the data linearizes the LWR and allows the impact of other factors on the slope and intercept of the LWR to be considered (Al Nahdi et al. 2016, Ogle 2018). The analysis first focused on whelks from Santa Barbara and San Diego for which both sex and location data had been collected. A full statistical model that included the impacts of sex, site, and interactions among these factors on the LWR was developed. Significance was assessed using F-tests, given $\alpha = 0.05$. Type III sums of squares were used in determining P values given differences in sample numbers among sites, and model assumptions were checked (Zuur et al. 2010). Given that whelks were collected at different times for each site and that LWR may vary across seasons, the model selection process was also repeated using only data from February 2011, a period when whelks were collected at both sites.

The same process was used to determine the impact of the site on the LWR, this time considering all collected whelks (from San Diego, Santa Barbara, and Monterey regions). Analyses were carried out in R version 4.2.2 (R Core Team 2022). Maps and graphs were produced using the rnaturalearth, ggplot2, ggforce, and ggrepel packages (Wickham 2016, Pedersen 2022, Massicotte & South 2023, Slowikowski 2023). Analyses used the car and nlstools packages (Florent et al. 2015, Fox & Weisberg 2019).

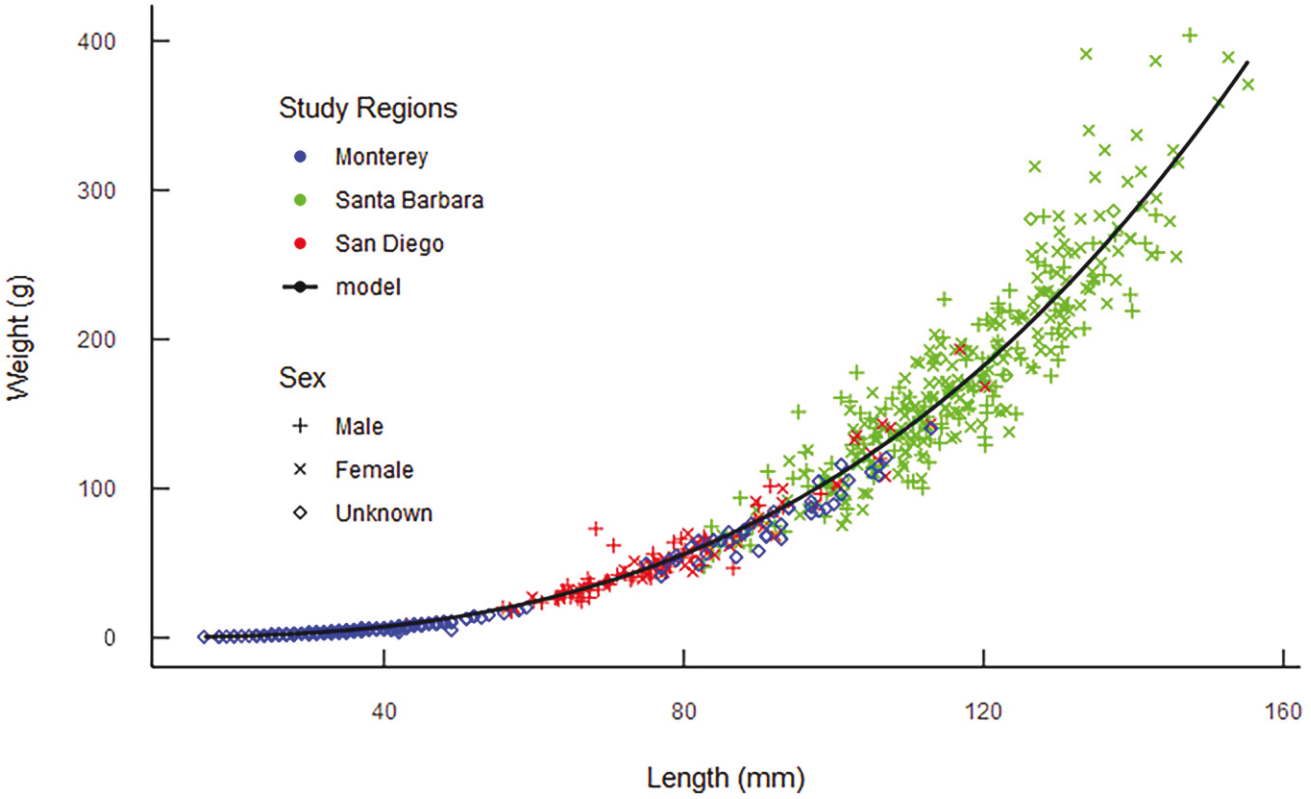

Figure 2. Empirical measurement and model fit of *Kelletia kelletii* weight (mass in g) and shell length (mm) from 2010 to 2011 collections at sites in California, USA. See Table 1 for equation details.

RESULTS

A total of 761 Kellet's whelks were obtained and analyzed: 119 from San Diego (4.36–12.02 cm, 9.91–193.38 g, 57 males, 60 females); 353 from Santa Barbara (7.93–15.53 cm, 47.63–403.89 g, 127 males, 218 females); and 289 from Monterey (1.60–11.30 cm, 0.51–140.26 g).

Analysis revealed the cubic function (AIC: 6,345.199) explained the LWR of the entire dataset better than a linear fit (AIC: 7,179.82) (Fig. 2) and had good explanatory power (pseudo-R^2 = 0.96). Parameter estimates of the *a* and *b* parameters from the model were found to be 0.0001598 and 2.913, respectively (Table 1).

Analysis of whelks of known sex and the collection site (from Santa Barbara and San Diego) indicated these factors did not impact the LWR. Only length was found to significantly predict weight (Table 2). Length was also found to be the only significant predictor when considering only whelks collected in February 2011, a period for which both sites were sampled (Table 2). A comparison of models focused on the full dataset also indicated that the collection site did not have a significant impact on the slope of the LWR, with length being the only significant predictor (Table 3).

TABLE 1.

Fitted parameters for the length-weight function $W = aL^b$ (n = 729, using all whelks with matched weight and length data).

		95% confidence interval	
Parameter	**Estimate**	**Lower**	**Upper**
a	0.0001598	0.0001010	0.0002186
b	2.913	2.837	2.990

DISCUSSION

This study revealed two simple and important findings regarding the LWR for Kellet's whelk: (1) Kellet's whelk exhibits a clear LWR following the standard cubic model ($W = aL^b$, R^2 = 0.96), and (2) the relationship appears to hold across sexes and collection regions.

An estimate of 3.0 for the exponential parameter *b* in the cubic model indicates organisms exhibit isometric growth, where length and width increase at the same rate (and thus changes in weight are related to the third power of length). This typically indicates body shape does not change as organisms grow. By contrast, this study revealed *b* values for *Kelletia kelletii* that were marginally lower than 3, indicating a slightly negative allometric pattern. This may occur if the shell length grows faster than the rate of increase of the width of the organism. Other marine gastropods have also demonstrated this growth pattern, including fished species of *Buccinum* and *Rapa* (focusing on wet tissue weight) (Ilano et al. 2004, Mann & Westcott 2006, Heude-Berthelin et al. 2011). Positive allometric growth, where width increases faster than length, and isometric relationships have also been observed in some gastropods (Elhasni et al. 2018, Ramses et al. 2019). LWRs may also vary among populations due to environmental factors. For example, predation pressure may lead to increases in

TABLE 2.

Statistical results for the models considering impacts of sex and site on LWR for subset of whelks with known sex (determined via dissection only for subsamples from Santa Barbara and San Diego).

Whelks with known sex (n = 431)				Only whelks collected in February (n = 212)			
Factor	**df**	F	P	**Factor**	**df**	F	P
Sex	1	2.33	0.13	Sex	1	0.09	0.76
Location	1	0.02	0.88	Location	1	1.65	0.2
log(Length)	1	1,014.40	**< 0.001**	log(Length)	1	174.49	**< 0.001**
Sex:Location	1	0.88	0.35	Sex:Location	1	0.06	0.81
Sex:log(Length)	1	2.43	0.12	Sex:log(Length)	1	0.13	0.72
Location:log(Length)	1	0.03	0.87	Location:log(Length)	1	1.58	0.21
Sex:Location:log(Length)	1	0.83	0.36	Sex:Location:log(Length)	1	0.08	0.77

Models considered all relevant data and samples collected in February. Listed are the sources of variation, degrees of freedom (df), F-ratio, and P value. P values < 0.05 are bolded.

TABLE 3.

Statistical results for the model considering impacts of site on LWR for all collected whelks with matched weight and length data.

Factor	**df**	F	P
log(Length)	1	2,216.55	**<0.001**
Location	2	2.09	0.12
log(Length):Location	2	1.10	0.33

Listed are the sources of variation, degrees of freedom (df), F-ratio, and P value. n = 729. P values < 0.05 are bolded.

shell thickness that cause width to increase faster than length (Elhasni et al. 2018).

The sex of whelks did not affect the slope or intercept of the LWR. Observations of mating pairs of Kellet's whelk in the wild have found females to typically be larger than males, and males become sexually mature at a smaller size than females (Rosenthal 1970, Cumberland 1995). Differences in size may be due to the time spent growing or rate of growth and thus not impact the relationship between size and weight. Differences in optimal size between the sexes and related selection pressure, however, could also impact the LWR, and previous research has noted differences in LWR relationships among sexes in gastropods (Hollander et al. 2006, Ramses et al. 2019). These factors suggest that future research on this topic is warranted.

The site also had no impact on the LWR. Previous research, however, found Kellet's whelk physiological performance and protein expression patterns to be affected by water temperature (Vasquez et al. 2019, Diaz et al. 2021), and pilot research found differences in the growth rate (change in size in relation to age) between Kellet's whelks from populations in the historical versus expanded range of the species (Rodriguez et al. 2015). Thus, further research on the effect of site on the LWR of the species is warranted, especially as populations become further established in the expanded range.

The samples used in this study were obtained opportunistically, creating an unbalanced sampling design in regard to the size and number of whelks collected at each site. Growth and LWRs may also vary across seasons due to water temperature, which may have also differed among the years specimens were collected, or due to factors such as gonad development. Although these features may limit the ability of the results to precisely parameterize differences in the LWR of the Kellet's whelk in relation to geography and sex, the data and tight fit of the model suggest these factors have minor impacts on the LWR of the species. The provided results thus offer valuable insight into an emerging fishery.

Future efforts should focus on concurrently collecting similarly sized whelks at multiple locations and sexing all collected individuals to fully consider the impacts of sex and site on the LWR. Sampling newly hatched or smaller specimens would be especially useful in considering differences in the intercept of the LWR across sites. Data collection on other biological factors of Kellet's whelk would further the value of the LWR presented here, because the LWR is often used in conjunction with other biological information on the species, such as individual growth rate, for supporting conservation and fisheries management of the species (Lester et al. 2018).

Marine molluscs represent a major category of fisheries species that provide an important food source worldwide (Alati et al. 2020). Across California, several molluscan species have high historical value as commercial and recreational fisheries species. Market squid (*Doryteuthis opalescens*) currently supports the second highest ex-vessel value commercial fishery in California (after Dungeness crab) and is the most valuable commercial fishery in several regions (e.g., Santa Barbara, CA) (CDFW 2020b, 2022). Unfortunately, marine molluscs are also vulnerable to overharvest. Multiple species are currently suffering from dramatic population declines, including the red abalone (*Haliotis rufescens*) and Pismo clam (*Tivela stultorum*) (Rogers-Bennett et al. 2013, Braje 2016). Consequently, developing essential biological information, such as LWRs, for marine molluscan fisheries species is of pressing importance (Phillips 1981, Rogers-Bennett et al. 2007). This study provides critical information for the emerging Kellet's whelk fishery and offers guidance for future research efforts.

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AUTHOR CONTRIBUTIONS

J.S.G., J.C., D.Z., and C.W. designed the project. J.S.G., J.C., and C.W. collected data. S.H., J.S.G., and C.W. analyzed the data. All authors contributed to manuscript development and editing.

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