Morphometric Relationships and Shell form of Cultured Winged Pearl Oysters (*Pteria penguin*) in Tonga

Author(s): Sophie E. Gordon, Poasi Ngaluafe, Max Wingfield and Paul C. Southgate
Source: Journal of Shellfish Research, 36(3):677-682.
Published By: National Shellfisheries Association
https://doi.org/10.2983/035.036.0317
URL: http://www.bioone.org/doi/full/10.2983/035.036.0317

Journal of Shellfish Research, Vol. 36, No. 3, 677–682, 2017.

MORPHOMETRIC RELATIONSHIPS AND SHELL FORM OF CULTURED WINGED PEARL OYSTERS (*PTERIA PENGUIN*) IN TONGA

SOPHIE E. GORDON,[1]* POASI NGALUAFE,[2] MAX WINGFIELD[3] AND PAUL C. SOUTHGATE[3]
[1]*Faculty of Science, Health, Education and Engineering, University of the Sunshine Coast, 90 Sippy Downs Drive, Sippy Downs, Queensland 4556, Australia;* [2]*Aquaculture Division, Ministry of Fisheries, Nuku'alofa, Tongatapu, Tonga;* [3]*Australian Centre for Pacific Islands Research and Faculty of Science, Health, Education and Engineering, University of the Sunshine Coast, 90 Sippy Downs Drive, Sippy Downs, Queensland 4556, Australia*

ABSTRACT Shell dimensions of 588 hatchery-produced *Pteria penguin* (Röding, 1798) were measured and analyzed to describe morphometric changes in shell form of this species over its life cycle. Oysters ranged from 9.4 to 202.2 mm in dorsoventral height (DVH), 0.1–1,526.9 g in weight and spanned 0.5–5 y of age. Significant positive curvilinear relationships were observed between shell width (SW) and DVH ($R^2 = 0.99$, $P < 0.001$), diagonal length (DL) and DVH ($R^2 = 0.99$, $P < 0.001$), shell thickness (ST) and DVH ($R^2 = 0.98$, $P < 0.001$), and wet weight (WW) and DVH ($R^2 = 0.99$, $P < 0.001$). Trends in the morphometric ratios of *P. penguin* indicated a proportional decrease in SW and DL with increasing DVH, resulting in a shift from a horizontally elongate to a vertically elongate shell form. The ST of *P. penguin* remained proportionally stable over its life cycle, whereas its WW increased proportionally by more than two orders of magnitude. Based on the results of this study, future research should examine (1) the relationship between the external shell dimensions and internal nacreous area, (2) changes in nacre deposition rate in different shell locations, and (3) the relationship between soft tissue weight, shell weight, nacre thickness, and DVH of *P. penguin*. The description of the growth form of *P. penguin* represents an important first step toward determining optimum half-pearl (mabé) culture procedures for *P. penguin* in Tonga.

KEY WORDS: pearl oyster, pearl production, shell dimensions, morphometrics, mabé, Tonga, *Pteria penguin*

INTRODUCTION

Pearl farming and associated activities provide an environmentally benign income source to many remote Pacific island communities (Southgate et al. 2008). The culture of half-pearls or "mabé" requires lower financial and technological investment, has a shorter culture duration than round pearl culture (Southgate et al. 2008, Kishore et al. 2015), and is compatible with the lifestyles of coastal communities in the Pacific. Mabé pearls result from the adhesion of plastic hemispherical nuclei to the inner shell surface of an oyster and the subsequent covering of each nucleus with nacre (mother of pearl) over a period of 5–12 mo (Ruiz-Rubio et al. 2006. Kishore et al. 2015). The winged pearl oyster *Pteria penguin* has been used to sustain an artisanal mabé pearl industry in Tonga since the species introduction in 1975 (Fa'anunu & Manu 1996, Teitelbaum & Fale 2008). The Tongan mabé pearl industry has significant development potential and has the capacity to provide broad livelihood benefits to the people of Tonga and generate estimated annual revenues of over US $7.5 million (Yamamoto & Tanaka 1997, Southgate et al. 2016). Whereas such development has been limited by the availability of wild-collected spat and adult oysters (Teitelbaum & Fale 2008, Southgate et al. 2016), recent improvements to hatchery procedures (Southgate et al. 2016) have increased the supply of oysters to pearl farmers. Hatchery-produced *P. penguin* now represent most of the oysters used for mabé production in Tonga. Accordingly, there is now a need to shift research focus toward understanding the effects of environmental and husbandry inputs on *P. penguin* performance in culture and mabé pearl quality.

Production of high-quality mabé pearls can only be achieved when the size, age, and growth form of the oyster are carefully considered (Saucedo et al. 1998, Ruiz-Rubio et al. 2006, Kishore et al. 2015). Throughout the life cycle of a pearl oyster (family Pteriidae), the morphometric relationships between shell dimensions vary to reflect biological and physiological changes (Galtsoff 1931, Alagarswami & Chellam 1977, Saucedo & Southgate 2008). These changes in shell morphology affect nacre deposition rates throughout the shell and, therefore, influence pearl quality by altering the pattern and rate of nacre deposition on implanted nuclei (Saucedo et al. 1998). The shell dimensions and growth form of a pearl oyster, therefore, have important implications for mabé pearl culture, ranging from the appropriate age and size of the oyster for seeding to the culture duration and the appropriate number and size of nuclei to be implanted (Saucedo et al. 1998, Ruiz-Rubio et al. 2006, Kishore et al. 2015). Accordingly, morphometric information has been used to make important recommendations about the ideal conditions for both round pearl and mabé pearl culture from pearl oysters (Saucedo et al. 1998, Linoy Libini et al. 2011, Serna-Gallo et al. 2014).

Although *Pteria penguin* is widely used for mabé pearl culture in Tonga, Japan, and a number of other countries (Southgate et al. 2008), there is a scarcity of published information describing changes in the morphometrics of this species, which have important implications for mabé pearl production (Saucedo et al. 1998). Whereas morphometric information has been previously presented for wild-collected *P. penguin* (Linoy Libini et al. 2011, Milione et al. 2011), similar information for hatchery-produced oysters or for locations in the Pacific has not previously been reported. This study aims to describe the relationships between the shell dimensions of hatchery-produced *P. penguin* in Tonga and use these relationships

---

*Corresponding author. E-mail: sophie.gordon@research.usc.edu.au
DOI: 10.2983/035.036.0317

as a tool to identify important research priories for improving the culture protocol for this species. Results will provide essential baseline information about this species and represent the first step toward determining the ideal conditions for mabé pearl culture using *P. penguin* in Tonga.

MATERIALS AND METHODS

Sampling and Measurements

The study was conducted at the Ministry of Fisheries, Aquaculture facility in Sopu, on the island of Tongatapu, Tonga (21°07′21″ S, 175°13′36″ W). The oysters used in this study ranged between 6 mo and approximately 5 y old and spanned the majority of the species life cycle from nursery stock to brood stock. The oysters were spawned at the Sopu aquaculture facility and were cultured using standard Ministry of Fisheries hatchery, grow out, and stock maintenance procedures (Southgate et al. 2016). All oysters were progressively grown out in oyster baskets and then in chaplets (>2 y old) at a depth of approximately 5 m on long lines adjacent to the aquaculture facility. The data used for this study were generated from measurements of 588 oysters that were randomly selected during routine stock maintenance activities.

Each oyster was cleaned of fouling and dabbed dry before six shell dimensions were measured: (1) dorsoventral height (DVH); (2) shell width (SW); (3) anterior–posterior length (APL); (4) diagonal length (DL); (5) shell thickness (ST); and (6) wet weight (WW). The visual and written definitions of each shell dimension are provided in Figure 1 and Table 1, respectively. A scaled photograph was then taken of each oyster from which DVH, SW, APL, and DL were measured to ±0.001 mm using the image processing software ImageJ (Schneider et al. 2012). Shell thickness was measured to ±0.1 mm using vernier calipers, whereas WW was measured to ±0.01 g with an electronic balance.

Statistical Analysis

The relationships between the shell dimensions of all oysters were examined to describe potential changes in the shell form of *Pteria penguin* over its life cycle. Dorsoventral height has been suggested to be the most representative measure of *P. penguin* growth (Milione et al. 2011) and so was used as the independent variable for all analysis. Regression analysis was used to examine relationships between DVH and the absolute and relative (ratio) values of each shell dimension. The relative value of each shell dimension was calculated by dividing the measurement (e.g., SW) by the DVH of each oyster to produce a ratio for each individual. Although the relationships between absolute shell dimensions were useful for describing the predictive relationships between shell dimensions, the trends were easily dominated by the effect of increasing scale. Accordingly, an examination of the relative values of shell dimensions (ratios) standardized for increasing shell size provided a clearer description of the overall changes in shell form throughout the life cycle of *P. penguin*.

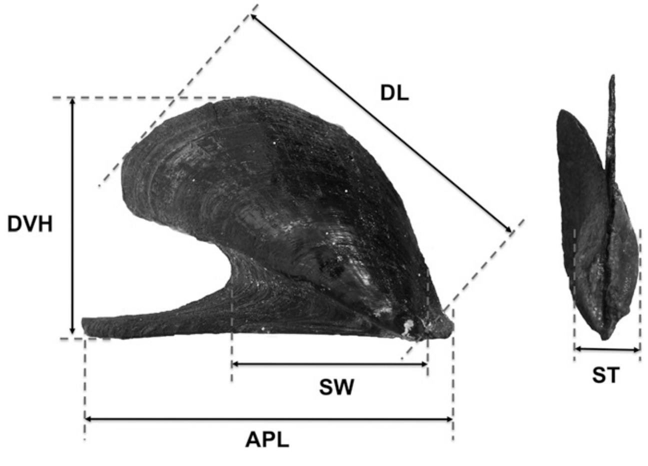

Figure 1. Shell dimensions: DVH, APL, SW, DL, and ST as applied to *Pteria penguin*.

Anterior–posterior length or hinge length is a fundamental shell dimension commonly used to describe the shell form of pearl oysters (Hynd 1955, Saucedo & Southgate 2008). It has been suggested, however, that APL is an unreliable measurement for *Pteria penguin* because the thin shell hinge of this species is prone to breakage (Linoy Libini et al. 2011). Oysters with recently broken hinges can be excluded from measurement (as in the present study), however it is very difficult to determine whether the APL of an older individual is due to changes in morphology or the result of previous damage. The relationship between APL and DVH was therefore examined (log-transformed data, $R^2 = 0.93$, $P < 0.001$, Fig. 2A) to enable comparison of this population with previous studies (Linoy Libini et al. 2011, Milione et al. 2011) but was not used for further analysis. A comparison of SW and APL additionally indicated that when the value of SW was subtracted from APL, the resulting value exhibited a weak, variable relationship with DVH (log-transformed data, $R^2 = 0.46$, $P < 0.001$, Fig. 2B). Accordingly, SW was selected as the appropriate shell dimension to describe the shell length of *P. penguin* in this study.

All measurements were log transformed to meet the statistical assumptions required for linear regression analysis (Whitlock & Schluter 2009). Linear models were fitted to the transformed data using a Gaussian distribution and were validated by examining the diagnostic plots of each model. Higher order polynomial regressions were fitted to the relationships where Akaike information criterion values indicated they were more favorable than linear regressions. The 95% prediction intervals of each model are presented because the 95% confidence intervals of most models were barely visible. The linear relationships between the log-transformed variables were rearranged to present power relationships relative to the untransformed data in the form of $y = ax^b$, where y is the dependent variable (e.g., SW), x is DVH and a and b are the y-intercept and slope, respectively. All analyses were completed in R (R Core Team 2017). Models were fit using base R and car (Fox & Weisberg 2011).

RESULTS

Absolute Shell Measurements

The oysters examined in this study ranged in size from 9.4 to 202.2 mm DVH, 10.5 to 147.0 mm SW, 17.0 to 279.7 mm APL, 16.0 to 277.0 m DL, 3.0 to 78.9 mm ST, and 0.1 to 1,526.9 g in

TABLE 1.

Definitions of the shell dimensions of *Pteria penguin* measured in this study.

Shell dimension	Definition
DVH	The greatest dimension of the oyster measured at a right angle to the hinge (Hynd 1955, Gervis & Sims 1992).
APL	The largest distance between the anterior and posterior shell margins parallel to the hinge (Hynd 1955, Gervis & Sims 1992).
SW	The minimum distance between the anterior and posterior shell margins parallel to the hinge.
DL	The greatest distance between the umbo and shell margin (Linoy Libini et al. 2011).
ST	The maximum distance between the external surfaces of the two shell valves when closed (Hynd 1955, Gervis & Sims 1992).
WW	The wet weight of the live oyster dabbed dry.

WW, and they spanned most of the growth of *Pteria penguin* from nursery stock to brood stock.

Regression analysis of absolute shell dimensions indicated the presence of strong significant positive curvilinear relationships between SW and DVH (log-transformed data, $R^2 = 0.99$, $P < 0.001$, Fig. 3A), DL and DVH (log-transformed data, $R^2 = 0.99$, $P < 0.001$, Fig. 3B), ST and DVH (log-transformed data, $R^2 = 0.98$, $P < 0.001$, Fig. 3C), and WW and DVH (log-transformed data, $R^2 = 0.99$, $P < 0.001$, Fig. 3D). Regression analysis also indicated that SW appears to reach a maximum width at approximately 170 mm DVH and does not increase in relation to DVH after this point (Fig. 3A). A separation of *Pteria penguin* brood stock (approximately 5-y old) from other oyster stocks was also evident in relation to both ST and WW (Fig. 3C, D). All brood stock exhibited a ST above approximately 60 mm and a WW of 600 g, whereas the oldest seeding stock (approximately 3.5-y old) exhibited a ST below 60 mm and a WW below 600 g (Fig. 3C, D). Brood stock were on average 2.16–2.33 times heavier than other oysters of the same DVH (Fig. 3D).

Relative Shell Measurements

The ratios of SW:DVH and DL:DVH both exhibited a significant negative curvilinear relationship with DVH (log-transformed data, $R^2 = 0.81$, $P < 0.001$, Fig. 4A; log-transformed data, $R^2 = 0.80$, $P < 0.001$, Fig. 4B, respectively). The average ratio (±SD) of SW:DVH declined from a maximum of 1.17 ± 0.11:1 (below 20 mm DVH) through 1:1 (at 30–40 mm DVH) to a minimum of 0.65 ± 0.03:1 (above 190 mm DVH). The DL:DVH ratio declined from a maximum of 1.74 ± 0.12:1 (below 20 mm DVH) to a minimum of 1.30 ± 0.05:1 (170–180 mm DVH). The ratio of ST:DVH exhibited a weak curvilinear relationship with DVH (log-transformed data, $R^2 = 0.32$, $P < 0.001$, Fig. 4C), indicating a weak negative relationship below approximately 90 mm DVH and a slight positive relationship above 90 mm DVH. The ratio of ST:DVH ranged from a minimum of 0.25 ± 0.02:1 (at 80–90 mm DVH) to a maximum of 0.37 ± 0.03:1 (at 180–190 mm DVH). The ratio of WW:DVH exhibited a significant positive curvilinear relationship with DVH (log-transformed data, $R^2 = 0.97$, $P < 0.001$, Fig. 4D) and increased from a minimum of 0.03 ± 0.01:1 (below 20 mm DVH) through 1:1 (at 90–100 mm DVH) to a maximum of 5.74 ± 1.11:1 (at 180–190 mm DVH).

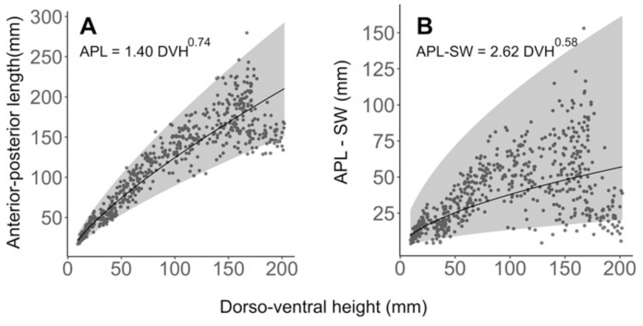

Figure 2. The curvilinear relationships between DVH and (A) APL and (B) APL – SW of cultured *Pteria penguin* ±95% prediction intervals.

The general change in the shell form of *Pteria penguin* over its life span in relation to DVH can therefore be described by an average proportional: (1) narrowing of SW by 44.4%; (2) shortening of DL by 25.3%; (3) stability of ST; and (4) an increase in WW by more than two orders of magnitude. These relative changes describe the shift from the horizontally elongate shell form of *P. penguin* nursery stock to the vertically elongate shell form of mature *P. penguin* brood stock (Fig. 5). The nature of these relationships indicate that *P. penguin* undergoes continuous change in the shell form throughout its life cycle in relation to SW, DL, and WW, whereas ST remains relatively stable and increases slightly above approximately 90 mm DVH.

DISCUSSION

This study has shown that significant curvilinear relationships exist between DVH and all other shell dimensions examined (SW, DL, ST, and WW) for *Pteria penguin*. These strong morphometric relationships support the suggestion that DVH is a representative measure of growth and a suitable predictor of the shell dimensions of *P. penguin* (Milione et al. 2011). The relationships described in this study are largely concordant with those reported for wild *P. penguin* populations from northern Australia (Milione et al. 2011) and the Andaman and Nicobar Islands (Linoy Libini et al. 2011). Results from these studies, however, were based on fewer oysters with an ST above 60 mm and a WW above 450 g (Linoy Libini et al. 2011, Milione et al. 2011). These differences in population morphology indicate that older oysters (>5 y old) may not have been sampled in previous studies and may suggest that mortality rates differ between wild and cultured populations. The wide range of WW between oysters of the same DVH may also indicate that at approximately 170–200 mm DVH, *P. penguin* reaches near-maximum size, and growth becomes primarily directed toward increasing weight. The growth of *P. penguin* is similar to that reported for other pearl oyster species, which

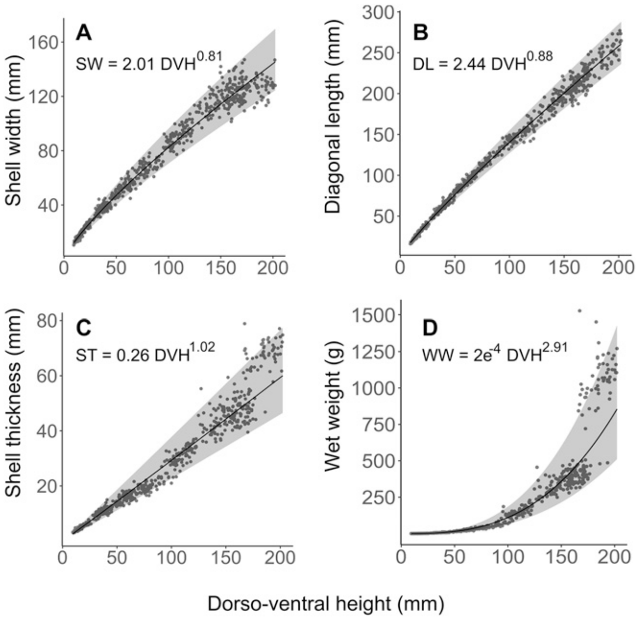

Figure 3. The curvilinear relationships between DVH and (A) SW, (B) DL, (C) ST, and (D) WW of cultured *Pteria penguin* ±95% prediction intervals.

demonstrate rapid increases in DVH in the first few years of growth followed by an increase in weight and ST (Gervis & Sims 1992, Gosling 2003).

The morphometric relationships of pearl oyster species are regularly used to deduce the optimal procedure for round pearl culture (Gervis & Sims 1992, Saucedo & Southgate 2008, Serna-Gallo et al. 2014). Trends in the external shell dimensions of pearl oysters have also been used to inform ideal culture conditions for mabé pearls (Saucedo et al. 1998, Linoy Libini et al. 2011). Because the culture of mabé pearls involves attaching the nuclei to the inner shell of the oyster (rather than implanting it within the tissue), the area of suitable inner shell surface cannot be overlooked as one of the most important factors dictating mabé pearl culture conditions (Saucedo et al. 1998, Ruiz-Rubio et al. 2006). This is particularly relevant for *Pteria penguin* because of its broad non-nacreous shell margin that results in the inner nacreous area of the shell being significantly smaller than the external shell dimensions; this feature of *P. penguin* is depicted well by Kishore et al. (2015). Accordingly, knowledge of the relationship between the external shell dimensions and the internal nacreous area of *P. penguin* is required before the results of this study are used to infer suggestions about mabé culture procedures.

Trends in the morphometric ratios of *Pteria penguin* indicated that this species changes from a horizontally elongate to a vertically elongate shell form throughout its life cycle. The relationships between the morphometric ratios and DVH of *P. penguin* suggest that this species undergoes a continuous proportional thinning of SW and a narrowing of DL throughout the growth, rather than an abrupt developmental change in morphology, as observed for *Pinctada mazatlanica* (Hanley, 1856) by Saucedo et al. (1998). The change in the shell form of *P. penguin* over its life cycle contrasts that of *Pteria sterna* (Gould, 1851) which shows a highly variable shell form and no clear growth trend (Saucedo et al. 1998). The growth form of *P. penguin* is instead more similar to that of *P. mazatlanica* and *Pinctada fucata* (Gould, 1850), which also become progressively more vertically elongate throughout their life cycle (Alagarswami & Chellam 1977, Saucedo et al. 1998). The consistency of the growth form of *P. penguin* suggests that recommendations about mabé pearl culture conditions will likely be applicable to the majority of individuals within the population. The growth pattern of *P. penguin* also indicates that the rate of nacre deposition at specific locations in the shell is likely to change over the life cycle of this species, resulting in the altered shell form (Gervis & Sims 1992, Saucedo et al. 1998). These changes in the pattern and rate of nacre deposition may, therefore, strongly influence the quality of mabé grown at different positions within the shell (Saucedo et al. 1998). Indeed, significant differences in mabé pearl quality have been identified between nucleus location within the shell of *P. penguin* (Kishore et al. 2015) and *P. sterna* (Ruiz-Rubio et al. 2006). Currently, no studies have examined the changes in nacre deposition rate at different shell locations over the life cycle of *P. penguin*.

Patterns in the morphometric ratios of *Pteria penguin* also indicate that ST remains relatively consistent throughout the life cycle of this species, whereas weight showed a consistent proportional increase. These trends are comparable to previous studies, which also observed minimal changes in relative ST with increasing DVH in wild populations (all ranging between 0.20 and 0.45:1; Linoy Libini et al. 2011, Milione et al. 2011). The present study did, however, detect a slight proportional increase in ST after approximately 90 mm DVH, which coincided with the first stage in the growth of the oyster where weight increased proportionally faster than DVH (when the WW:DVH ratio exceeded 1:1). This developmental stage may reflect a period of increased energetic allocation toward soft tissue growth or gamete production and may also include increased nacre secretion (Gervis & Sims 1992, Saucedo & Southgate 2008). Indeed, in

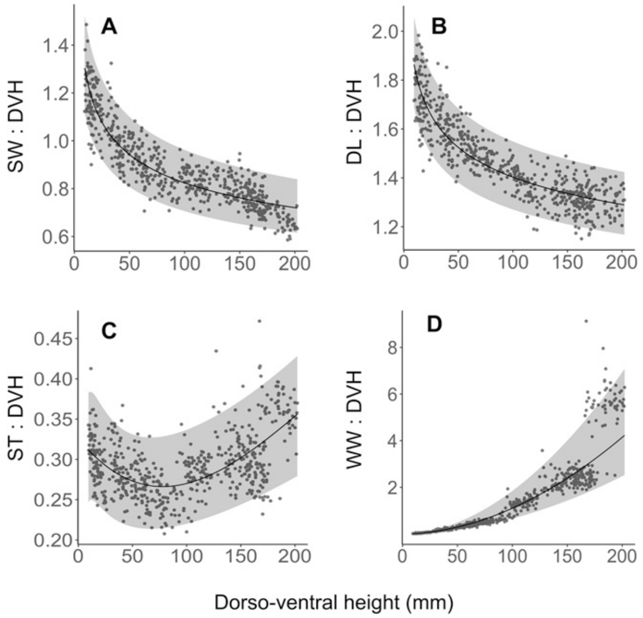

Figure 4. The curvilinear relationships between DVH and the ratio of (A) SW:DVH, (B) DL:DVH, (C) ST:DVH, and (D) WW:DVH of cultured *Pteria penguin* ±95% prediction intervals.

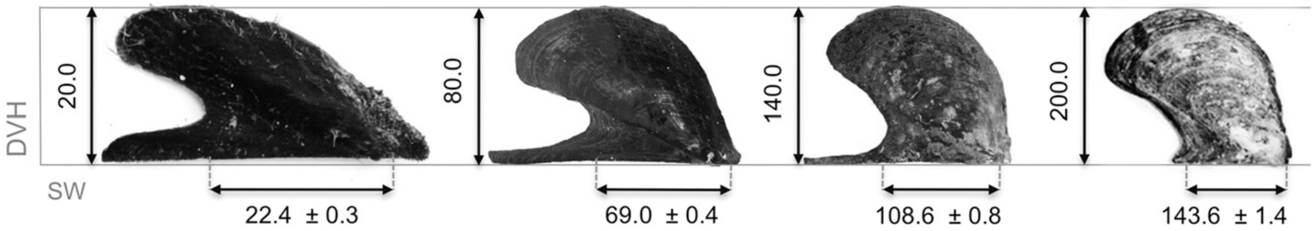

Figure 5. The general change in shell form of *Pteria penguin* between 20 and 200 mm DVH (mm) and the corresponding SW (mm ± SE). All images are scaled to a standard DVH to allow comparison.

Australian populations, female sexuality of *P. penguin* is first observed at approximately 90 mm DVH (Milione et al. 2011). Because current measurements did not distinguish between shell and soft tissues of the oysters, the biological mechanisms behind the morphometric trends in ST and WW can only be speculated. Accordingly, the relationships between DVH and shell weight, soft tissue weight and nacre thickness of *P. penguin* should be examined separately to better understand the mechanisms of these morphometric trends.

This study described the strong relationships present between the shell dimensions of *Pteria penguin* and demonstrated that this species changes from a horizontally elongate to a vertically elongate shell form throughout its life cycle. The description of the growth form of *P. penguin* provides essential baseline information about this species and represents an important first step toward determining an optimal mabé pearl culture procedure for this species in Tonga. The conclusions made from the present study were limited by the use of live oysters, which prevented the measurement of the internal nacre area, nacre thickness, and weight of the soft tissue and shell. Accordingly, future research should examine (1) the relationship between the external shell dimensions and internal nacreous area of *P. penguin*; (2) changes in nacre deposition rate at different locations within the shell of *P. penguin* over its life cycle; and (3) the relationship between soft tissue weight, shell weight, nacre thickness, and DVH of *P. penguin*. Elucidating the relationships between these internal metrics and the external shell dimensions of *P. penguin* will further support development of an optimal mabé pearl culture procedure for this species in Tonga, stimulating further industry development.

ACKNOWLEDGMENTS

The authors thank the staff of the Aquaculture Division of the Ministry of Fisheries, Tonga: Tracy Aisea, Tonga Tuiano, Siaosi Vi, Siaosi Fonua, Tevita Havea, and Setaleki Mafi, as well as the Halaevalu Mata'aho Marine Discovery Centre for their assistance with this study. This study was jointly funded by the University of the Sunshine Coast Graduate Research School and the Australian Centre for International Agricultural Research (ACIAR) and was conducted as part of ACIAR Project FIS/2016/126 "Half pearl industry development in Tonga and Vietnam" led by PCS at the University of the Sunshine Coast.

LITERATURE CITED

Alagarswami, K. & A. Chellam. 1977. Change of form and dimensional relationship in the pearl oyster *Pinctada fucata* from Gulf of Mannar. *Indian J. Fish.* 24:1–14.

Fa'anunu, U. & N. Manu. 1996. Aquaculture development in Tonga. In: Integrated fisheries survey report. Nukualofa, Tonga: Ministry of Fisheries and Japan International Cooperation Agency (JICA). pp. 70–75.

Fox, J. & S. Weisberg. 2011. An R companion to applied regression, 2nd edition. Thousand Oaks, CA: Sage.

Galtsoff, P. S. 1931. The weight-length relationship of the shells of the Hawaiian pearl oyster, *Pinctada* sp. *Am. Nat.* 65:423–433.

Gervis, M. H. & N. A. Sims. 1992. The biology and culture of pearl oysters (Bivalvia: Pteriidae). Metro Manila: ICLARM. pp. 9–38.

Gosling, E. 2003. Bivalve molluscs biology ecology and culture. Oxford, UK: Blackwell Science.

Hynd, J. S. 1955. A revision of the Australian pearl-shells, genus *Pinctada* (Lamellibranchia). *Aust. J. Mar. Freshwater Res.* 6:98–137.

Kishore, P., P. Southgate, P. Seeto & J. Hunter. 2015. Factors influencing the quality of half-pearls (mabé) produced by the winged pearl oyster, *Pteria penguin* (Röding, 1758). *Aquacult. Res.* 46:769–776.

Linoy Libini, C., K. J. Abraham, K. Shanmugam, K. Prakash Rao, V. Kripa, T. S. Velayudhan & K. S. Mohamed. 2011. Biometric relationships of the black winged pearl oyster, *Pteria penguin* (Röding, 1798) from Andaman and Nicobar Islands. *Indian J. Fish.* 58:139–143.

Milione, M., P. Saucedo & P. Southgate. 2011. Sexual development, sex ratio and morphometrics of *Pteria penguin* (Bivalvia: Pteriidae), in north-eastern Australia. *Molluscan Res.* 31:30–36.

R Core Team. 2017. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Available at: www.r-project.org.

Ruiz-Rubio, H., H. Acosta-Salmoìn, A. Olivera, P. C. Southgate & C. Rangel-Daìvalos. 2006. The influence of culture method and culture period on quality of half-pearls ('mabé') from the winged pearl oyster *Pteria sterna*, Gould, 1851. *Aquaculture* 254:269–274.

Saucedo, P., M. Monteforte & F. Blanc. 1998. Changes in shell dimensions of pearl oysters, *Pinctada mazatlanica* (Hanley 1856) and *Pteria sterna* (Gould 1851), during growth as criteria for Mabé pearl implants. *Aquacult. Res.* 29:801–814.

Saucedo, P. & P. C. Southgate. 2008. Reproduction, development and growth. In: Southgate, P. C. & J. S. Lucas, editors. The pearl oyster. Oxford, UK: Elsevier. pp. 161–177.

Schneider, C. A., W. S. Rasband & K. W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* 9:671–675.

Serna-Gallo, I., J. M. J. Ruíz-Velazco, H. Acosta-Salmón, E. Peña-Messina, G. Torres-Zepeda & P. E. Saucedo. 2014. Growth and reproduction patterns of the winged pearl oyster, *Pteria sterna* cultivated in tropical environments of Mexico: implications for pearl farming. *Cienc. Mar*. 40:75–88.

Southgate, P. C., A. C. Beer & P. Ngaluafe. 2016. Hatchery culture of the winged pearl oyster, *Pteria penguin*, without living micro-algae. *Aquaculture* 451:121–124.

Southgate, P. C., E. Strack, A. Hart, K. T. Wada, M. Monteforte, M. Carino, S. Langy, C. Lo, H. Acosta-Salmoìn & A. Wang. 2008. Exploitation and culture of major commercial species. In: Southgate, P. C. & J. S. Lucas, editors. The pearl oyster. Oxford, UK: Elsevier. pp. 303–355.

Teitelbaum, A. & P. Fale. 2008. Support for the Tongan pearl industry. *SPC Pearl Oyster Inf. Bull*. 18:11–14.

Whitlock, M.C & D. Schluter. 2009. The analysis of biological data. Greenwood village, CA: Roberts and Company Publishers.

Yamamoto, T. & H. Tanaka. 1997. Potential of commercial development of mabé pearl farming in Vava'u islands, Kingdom of Tonga (field document no. 5). South Pacific Aquaculture Development Project (Phase II), Food and Agriculture Organization of the United Nations (GCP/RAS/116/JPN), Suva, Fiji.