

Article

Age Structure and Growth Responses of the Pearl Oyster (*Pinctada radiata*) Under Contrasting Salinity Regimes in Bahrain Waters, Arabian Gulf

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Abstract

Understanding age and growth in marine bivalves is essential for interpreting population dynamics and environmental responses. The analysis of sclerochronological growth increments within internal shell layers provides a reliable approach for reconstructing age and growth history and preserves long-term records of environmental variability and stress. This study presents the first assessment of age structure and growth history of the pearl oyster *Pinctada radiata* in Bahrain waters using shell growth-line analysis. Pearl oysters from two contrasting salinity regimes in Bahrain waters, the Northern Area (~40‰) and the hypersaline Western Coast (~55‰), were examined using acetate peel replicas and internal shell growth-line analysis. Age determination was conducted from shell cross-sections, and growth patterns were evaluated through morphometric analysis and von Bertalanffy growth modelling. Oysters from the Northern Area attained larger shell sizes and exhibited estimated life spans of up to 5–6 years, whereas hypersaline populations displayed reduced life spans (3–4 years), thinner shells, and lower asymptotic growth despite rapid early development. A strong correlation between shell height and umbo height supported the reliability of internal growth increments as age proxies. These findings suggest that pearl oysters inhabiting naturally hypersaline habitats may exhibit a dwarf-like growth pattern and reduced life span associated with persistent hypersalinity. The results improve understanding of growth responses and physiological limits of *P. radiata* under naturally hypersaline conditions in the Arabian Gulf.

Keywords: *Pinctada radiata*; pearl oyster; age determination; sclerochronology; growth responses; salinity stress; hypersaline habitats; physiological dwarfism; shell biomineralization; Arabian Gulf



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1. Introduction

Marine bivalves play important ecological roles in coastal ecosystems and contribute significantly to the structure and functioning of benthic communities [1–3]. Reliable age determination is fundamental for understanding population dynamics, growth processes, life-history characteristics, and environmental influences on bivalve populations [4,5]. Sclerochronological analyses of periodic growth lines preserved within calcified shell structures provide a reliable approach for reconstructing age, growth history, and environmental variability in marine bivalves [6–8].

The pearl oyster *Pinctada radiata* (Leach, 1814) is an ecologically and economically important bivalve throughout the Arabian Gulf, particularly in Bahrain waters, where it supports a historically significant pearling industry, cultural heritage, and ongoing initiatives to revive and sustain the natural pearling sector [9]. Despite this importance, information on age structure, longevity, and growth responses of wild populations remains limited, especially under naturally hypersaline environmental conditions.

Periodic shell-increment deposition reflects endogenous biological processes and external environmental drivers, including temperature, salinity, and food availability, thereby preserving chronological records of growth and habitat conditions [10,11]. Shell accretion is controlled by mantle-mediated biomineralization processes, in which organic matrix proteins regulate calcium carbonate formation and deposition within the shell [12]. Internal growth-line analyses have been widely applied in bivalves and contribute to ecological, fisheries, archaeological, and palaeoenvironmental investigations [6,13]. However, age structure and growth responses of *P. radiata* populations in Bahrain waters remain unexplored.

The Arabian Gulf is characterized by extreme environmental conditions, including high summer temperatures and elevated evaporation rates that generate some of the highest marine salinities recorded worldwide [14]. Average salinity is approximately 40‰ but exceeds 50‰ in shallow embayments and coastal lagoons due to intense evaporation and restricted water circulation [14–16]. Within Bahrain waters, salinity varies substantially among habitats, ranging from approximately 40‰ in the Northern Area to hypersaline values exceeding 55‰ along the Western Coast [15,16]. Salinity strongly influences bivalve physiology and osmoregulation [17], as well as shell biomineralization, energy allocation, and growth [18]. Elevated salinity may constrain somatic growth, alter shell morphology, and reduce life span through increased physiological costs associated with osmoregulation and metabolic maintenance [19,20].

Seawater temperatures commonly exceed 36 °C during summer and fall below 20 °C during winter [14,16], producing annual cycles of accelerated and reduced shell deposition. These seasonal interruptions generate distinct internal growth lines that serve as chronological markers in *P. radiata*, enabling reconstruction of age, growth history, and environmental variability [10,21].

Earlier biological studies in Bahrain provided important baseline information on the biology, reproduction, and morphometric characteristics of *P. radiata* [22], while recent literature has highlighted its economic, heritage, and biological importance [9]. However, age estimation has largely relied on shell-size or length-based classification rather than direct internal growth-line analysis. Consequently, sclerochronology-based assessment of age structure, life span, and growth responses under contrasting salinity regimes remains limited. This gap is important for understanding environmental controls on pearl oyster growth and supporting future conservation, monitoring, and management initiatives.

Therefore, this study uses acetate peel replicas and internal shell growth-line analysis to investigate age structure and growth responses of *P. radiata* populations inhabiting two contrasting salinity regimes in Bahrain waters. Specifically, the study aims to (i) determine age structure and life span, (ii) characterize growth patterns using morphometric relationships and von Bertalanffy growth modelling, and (iii) evaluate the influence of contrasting salinity regimes on shell growth and development. The results provide the first sclerochronology-based assessment of age and growth in *P. radiata* from Bahrain waters and offer new insights into growth responses under naturally hypersaline conditions in the Arabian Gulf.

2. Materials and Methods

2.1. Study Area

The study was conducted in Bahrain waters, Arabian Gulf, using natural populations of the pearl oyster *Pinctada radiata* (Leach, 1814) collected from two habitats characterized by contrasting salinity regimes (Figure 1). The first site was the Northern pearl oyster beds (Hayr Bu Amamah) ($26^{\circ}47.389' \text{ N}$, $50^{\circ}49.502' \text{ E}$), one of Bahrain's principal offshore pearl oyster grounds and one of the historically recognized Bahraini oyster beds [23], where mean salinity was approximately 40‰ during the 12-month pre-collection period. The second site was located on the Western Coast near Yasuf Island ($26^{\circ}06.452' \text{ N}$, $50^{\circ}26.276' \text{ E}$), a naturally hypersaline habitat where salinity ranged from 53–57‰ during the same pre-collection period.

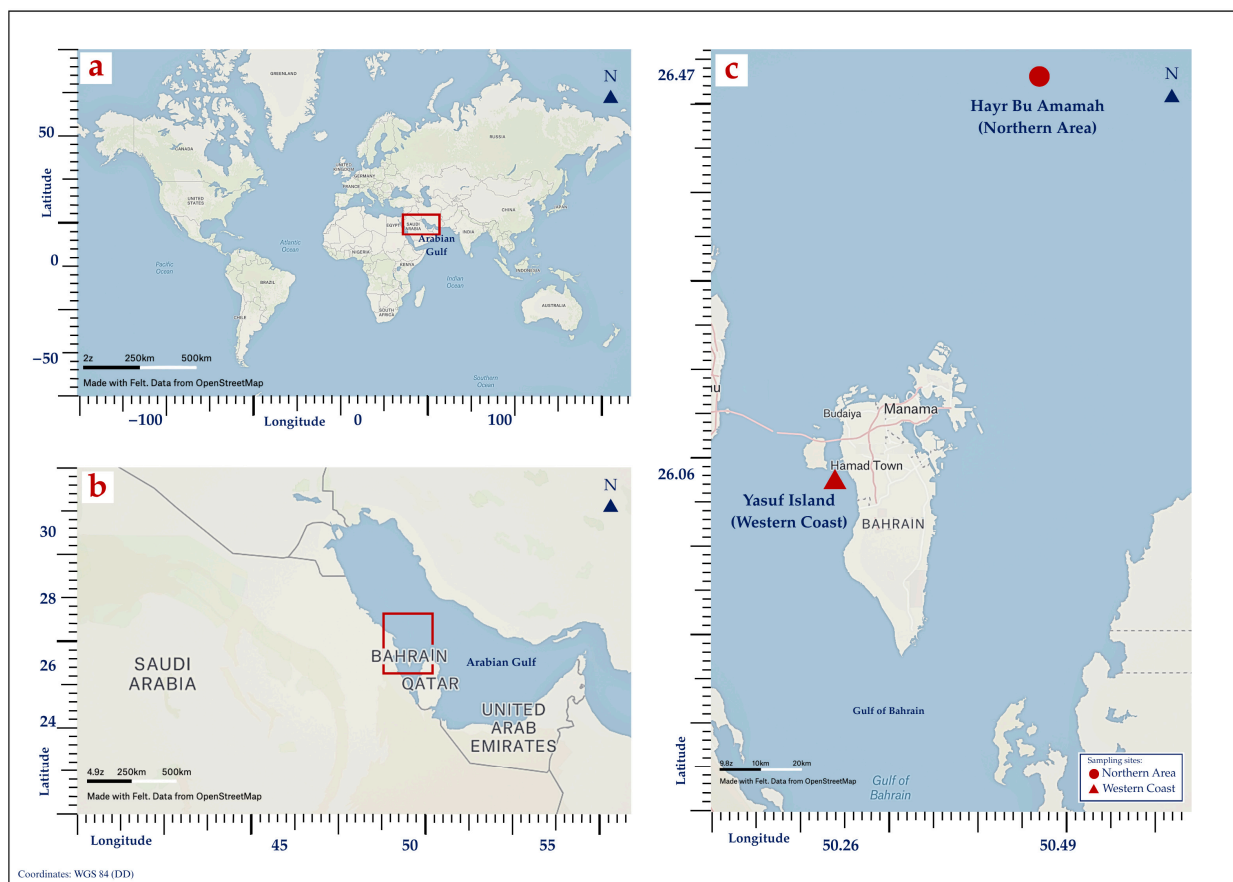


Figure 1. Study area showing the sampling locations of *Pinctada radiata* populations in Bahrain waters. (a) Location of the Arabian Gulf within the global context; (b) Location of Bahrain within the Arabian Gulf; (c) Sampling locations at the Northern Area (Hayr Bu Amamah) and the Western Coast (Yasuf Island). The map was prepared using Felt, with basemap data from OpenStreetMap.

The Arabian Gulf is characterized by extreme environmental conditions, including high seasonal temperature fluctuations, elevated evaporation rates, and some of the highest marine salinities recorded worldwide [14,24,25]. These environmental gradients provide a suitable natural system for evaluating the influence of salinity on age structure and growth characteristics of *P. radiata* populations.

2.2. Sample Collection and Morphometric Measurements

Pearl oyster specimens were collected during SCUBA surveys conducted in June 2022 following a standard underwater belt transect methodology [26,27]. At each site, a 20 m × 4 m belt transect was established, within which twelve 1 m² quadrats were examined at regular intervals for oyster counts and specimen collection. Habitat characteristics, substrate composition, and associated ecological features were recorded at each sampling location. Water depth was measured using a Suunto Zoop Novo dive computer (Suunto Oy, Vantaa, Finland), while visibility was estimated using a 20 cm Secchi disc. Seawater temperature and pH were measured in situ using a Thermo Scientific Orion Star A121 portable pH meter (Thermo Fisher Scientific Inc., Ayer, MA, USA), and dissolved oxygen was measured using a Thermo Scientific Orion Star A223 dissolved oxygen meter (Thermo Fisher Scientific Inc., Ayer, MA, USA). Salinity was determined using an ATAGO S/Mill refractometer (ATAGO Co., Ltd., Tokyo, Japan). Representative habitat conditions were documented using a GoPro HERO3+ camera (GoPro, Inc., San Mateo, CA, USA). Monthly salinity records collected during the 12 months prior to specimen collection were compiled to characterize site-specific salinity regimes. Collected oysters were placed in labelled mesh collection bags, transferred to insulated containers with ice, transported to the laboratory, cleaned of epibionts and debris, labelled, catalogued, measured for shell height and shell thickness, and stored under controlled laboratory conditions for subsequent age and growth analyses.

A total of 67 pearl oysters were analyzed, comprising 44 specimens collected from the Northern Area and 23 specimens from the Western Coast. The Northern Area population was represented by specimens collected from Hayr Bu Amamah, whereas the Western Coast population was obtained from Yasuf Island. Specimens representing the size range observed at each location were selected for subsequent age determination and growth analyses.

For each specimen, shell height (SH) was measured to the nearest 0.1 mm using digital callipers. Shell thickness was measured at the maximum valve thickness near the umbonal region prior to shell sectioning using a digital Mitutoyo calliper (Mitutoyo Corporation, Kawasaki, Kanagawa, Japan) with a precision of 0.01 mm. Additional morphometric measurements, including umbo height (UH), were obtained from shell cross-sections using a stereoscopic microscope equipped with a Nikon optical system and NIS-Elements image analysis software (version 5.30.00, Nikon Corporation, Tokyo, Japan), allowing measurements and image acquisition at micrometre resolution.

2.3. Shell Preparation and Acetate Peel Technique

Age determination followed the sclerochronological methodology described by Al-Mohannadi [28]. The left valve of each oyster was selected for analysis. The umbo region was cut using a diamond saw and embedded in Metaset resin prior to sectioning (Figure 2). Embedded specimens were sectioned through the umbo along the principal growth axis (X–Y) to expose internal shell structures associated with shell growth and age determination.

The exposed shell surfaces were progressively ground using calcined aluminium oxide (BDH Chemicals Ltd., Poole, UK) and polished to obtain a smooth section. The prepared sections were etched in 2% hydrochloric acid (HCl; EMSURE®, Merck KGaA, Darmstadt, Germany) for one minute, rinsed immediately with distilled water to remove reaction residues, and allowed to air dry. Acetate peel impressions were subsequently prepared using 35 µm cellulose acetate sheets and acetone (EMSURE®, Merck KGaA, Darmstadt, Germany) following established procedures [28].

The acetate peels were mounted on glass slides and examined under transmitted-light microscopy at magnifications of $40\times$ and $100\times$. This procedure enabled clear visualization of internal shell microstructures and annual growth lines used for age determination and growth reconstruction.

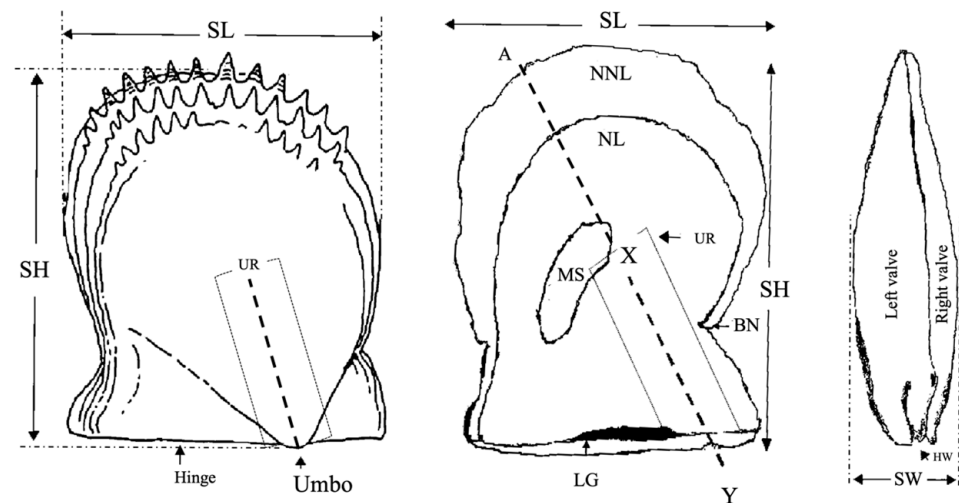


Figure 2. Schematic representation of *Pinctada radiata* shell morphology and sectioning procedure used for age determination, showing shell length (SL), shell height (SH), shell width (SW), hinge width (HW), umbo region (UR), non-nacreous layer (NNL), nacreous layer (NL), muscle scar (MS), byssal notch (BN), ligament groove (LG), hinge, and umbo. The dashed X–Y line indicates the principal sectioning axis through the umbo region used to expose internal growth structures for age determination. Arrows indicate the direction and extent of the corresponding shell measurements. Adapted from Gervis and Sims [2], Al-Mohannadi [28], Tlig-Zouari et al. [29], and Smyth et al. [30].

2.4. Age Determination and Growth-Line Analysis

Age estimates were obtained by counting visible annual growth increments preserved within shell cross-sections. Growth lines were examined primarily within the middle shell layer extending from the umbo region towards the shell margin, where annual growth bands were most clearly expressed (Figure 3). Similar annual growth-line periodicity has previously been reported for *P. radiata* inhabiting the Arabian Gulf [28,30].

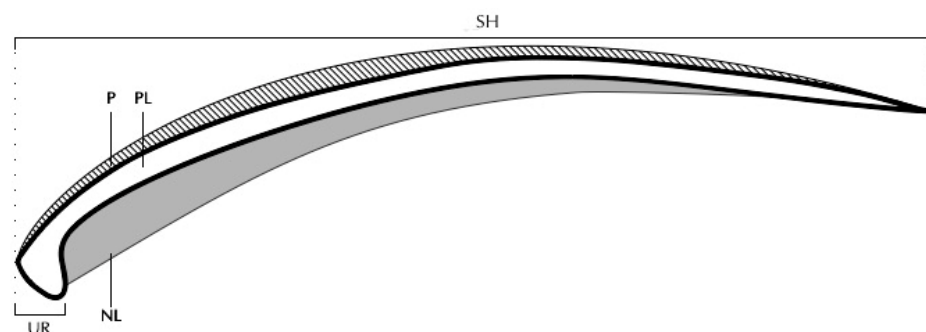


Figure 3. Cross-sectional structure of *Pinctada radiata* shell showing the periostracum, prismatic layer, nacreous layer, shell height, and umbo region used for age determination. Outer layer: Periostracum (P); Middle layer: Prismatic layer (PL); Inner layer: Nacre layer (NL); Shell height (SH); Umbo region (UR).

Visible growth increments were counted under microscopic examination and assigned to age classes. Measurements of umbo height corresponding to successive annual increments were recorded to reconstruct individual growth histories. As shell height at previous ages could not be measured directly from the shell exterior, the relationship between umbo height (UH) and shell height (SH) was established using oysters spanning a wide size range. Regression equations were subsequently used to estimate shell height corresponding to each annual growth increment following the procedure described by Al-Mohannadi [28]. Reconstructed age-length data derived from annual growth increments were used for growth curve modelling and comparative growth analyses between populations.

2.5. Growth Curve Modelling

Growth patterns were described using the von Bertalanffy Growth Function (vBGF) [4,5]:

$$L_t = L_{\infty} \left(1 - e^{-K(t - t_0)} \right)$$

where L_t is the shell height at age t , L_{∞} is the asymptotic shell height, K is the growth coefficient describing the rate at which the asymptotic size is approached, and t_0 is the theoretical age at zero length.

The parameter t_0 was fixed at 0 in all model fits, as the reconstructed age-length data were derived from discrete growth-line classes beginning with the zero-line group, which represented the observed baseline condition prior to the first visible annual growth increment. Age-shell height data reconstructed from annual growth-line measurements were fitted to the model to estimate growth parameters for each population.

2.6. Statistical Analysis

Linear regression and Pearson correlation analyses were used to examine relationships between shell height (SH) and umbo height (UH) in each population. Morphometric variation between populations was visualized using scatter plots with fitted regression lines and 95% confidence ellipses. Descriptive statistics, including mean, standard deviation (SD), and range, were calculated for shell thickness and growth-line measurements. Statistical analyses were performed using Minitab (version 21.1.0) and Python (version 3.11.11), while Microsoft Excel (version 16.94) was used for data preparation. Statistical significance was assessed at $\alpha = 0.05$. Given the unequal sample sizes between the Northern Area ($n = 44$) and Western Coast ($n = 23$), the statistical analyses were interpreted with caution. The strong SH–UH correlations and the agreement between observed and modelled growth patterns supported the comparative assessment, while sample-size imbalance was considered when interpreting population-level differences.

3. Results

3.1. Environmental Characteristics

Environmental conditions differed markedly between the two study areas (Figure 4). The Northern Area was characterized by offshore pearl oyster beds associated with rock, sand, and biogenic veneer substrates at a depth of 14 m, whereas the Western Coast comprised a shallow mixed habitat of pearl oyster beds, seagrass, macroalgae, and sandy-rock substrates at a depth of 2.5 m. Mean salinity was higher on the Western Coast (55.0‰) than in the Northern Area (39.0‰), while seawater temperature was broadly similar between sites (30 °C vs. 29 °C, respectively). Dissolved oxygen and pH were 7.40 mg L^{−1} and 7.50 on the Western Coast, compared with 7.20 mg L^{−1} and 6.90 in the Northern Area.

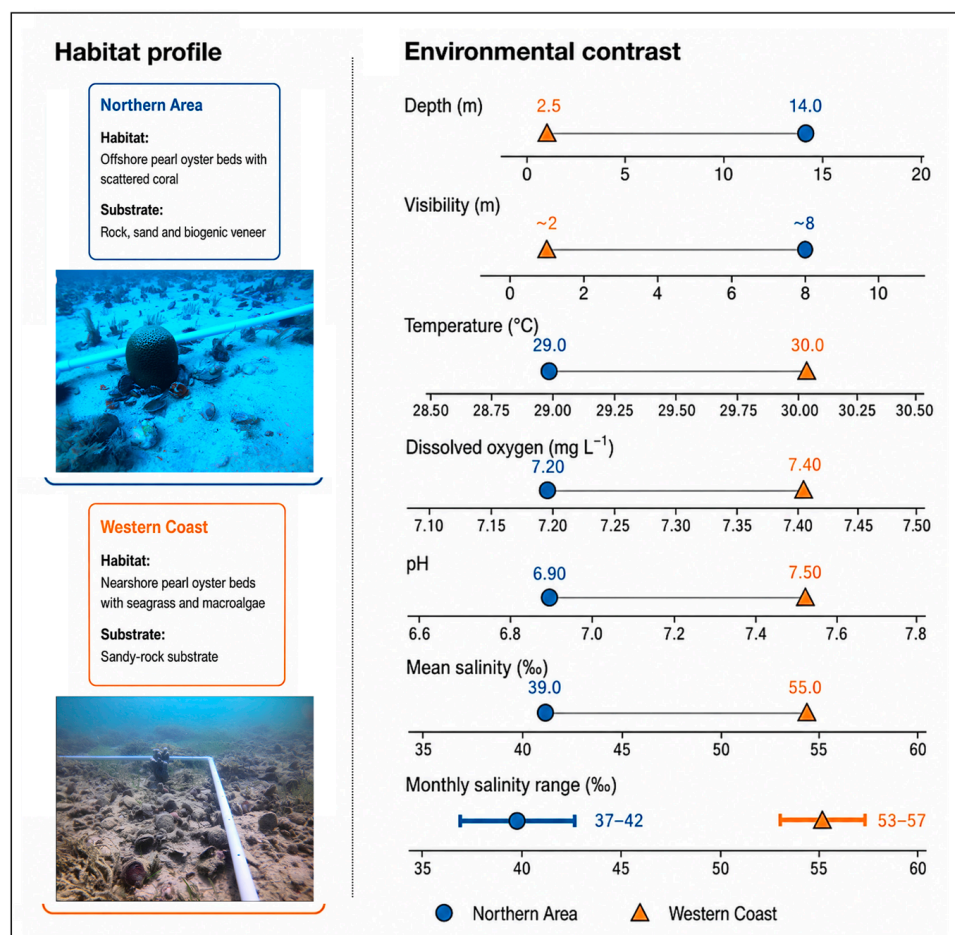


Figure 4. Environmental and habitat profile of the Northern Area and Western Coast sampling sites.

Monthly salinity records from the 12 months preceding specimen collection ranged from 37.0 to 42.0‰ in the Northern Area and from 53.0 to 57.0‰ on the Western Coast (Figure 5).

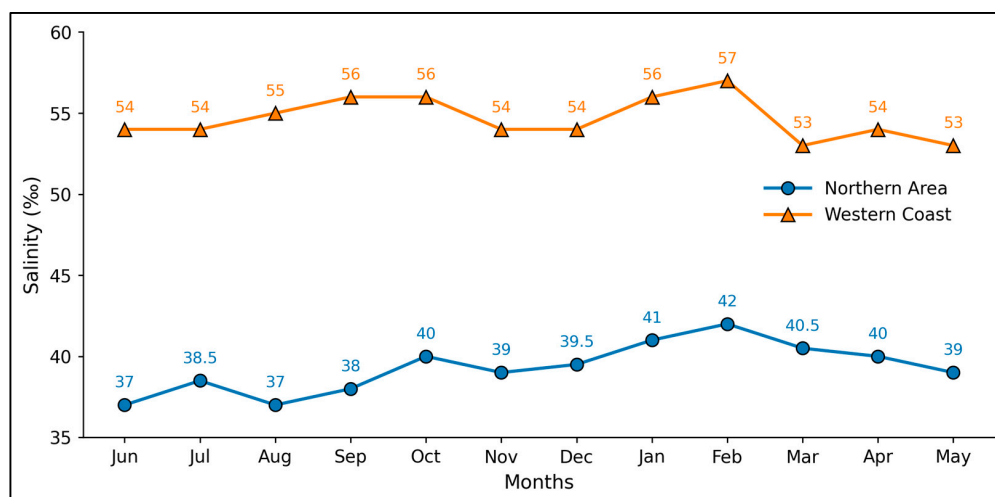


Figure 5. Monthly salinity regimes of the Northern Area and Western Coast during the 12 months prior to pearl oyster collection.

3.2. Size Frequency Distribution

Size-frequency distributions differed between populations (Figure S1). Northern Area pearl oysters exhibited a broader size range, with the majority represented within the 60–81 mm shell height classes. In contrast, Western Coast pearl oysters were dominated by smaller size classes, with the highest frequencies recorded between 31 and 50 mm shell height.

3.3. Shell Morphology of *Pinctada radiata*

Northern Area pearl oysters attained larger shell dimensions, with the largest individual examined measuring 88.34 mm in shell height, whereas the largest Western Coast individual measured 54.43 mm. Shell thickness was also greater in Northern Area oysters (3.81 ± 2.24 mm; range 0.79–10.68 mm) than in Western Coast oysters (2.15 ± 0.71 mm; range 0.94–3.17 mm).

Examination of both inner and outer shell surfaces revealed the characteristic morphology of *P. radiata* in both populations, including nacreous internal surfaces, asymmetrical valves, and clear differences in shell size, width, thickness, and the extent of the internal nacreous layer. Northern Area specimens displayed a broader morphological range, with larger valves and greater variation in shell thickness compared with Western Coast specimens. In contrast, Western Coast oysters were represented by smaller, thinner, and more compact shells within the examined sample. These observations provided an initial visual indication of the contrasting growth characteristics subsequently documented through growth-line analyses.

Representative shells collected from the two study populations exhibited noticeable differences in overall shell size and morphology (Figure 6).

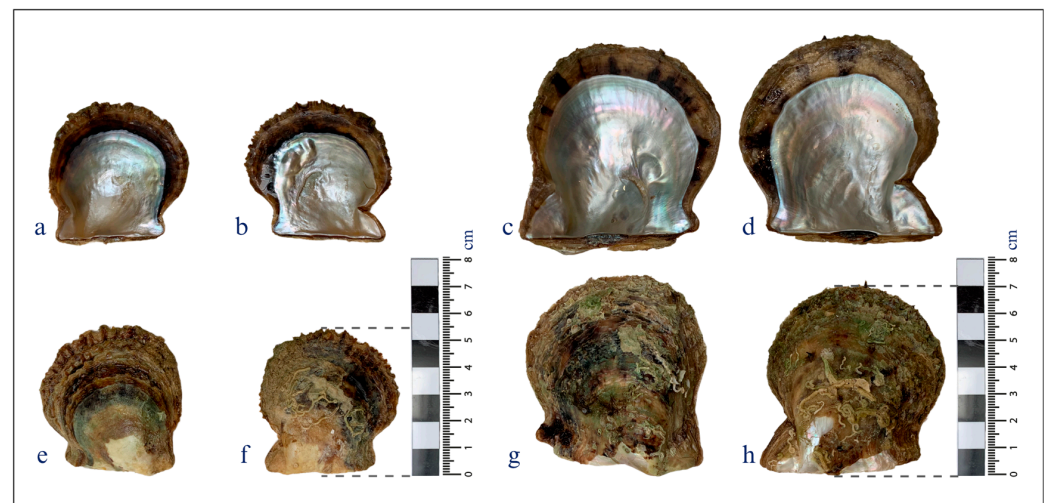


Figure 6. Representative shells of *Pinctada radiata* from the Western Coast and Northern Area populations. One of the largest Western Coast specimens (SH = 54.43 mm) shows the inner surfaces of the left (a) and right (b) valves and the outer surfaces of the left (e) and right (f) valves. A representative Northern Area specimen (SH = 69.61 mm) shows the inner surfaces of the left (c) and right (d) valves and the outer surfaces of the left (g) and right (h) valves.

3.4. Shell Structure and Growth Increment Identification

Cross-sectional examination of *Pinctada radiata* shells revealed a distinct shell structure consisting of an outer periostracum, a middle prismatic layer, and an inner nacreous layer (Figures 2 and 3). Annual growth increments were primarily observed within the prismatic layer extending from the umbo region towards the shell margin, providing the basis for age determination and growth reconstruction.

The visibility of growth increments varied among specimens and increased with shell size and age. No distinct annual growth lines were observed in young individuals with small shell dimensions (Figure 7).

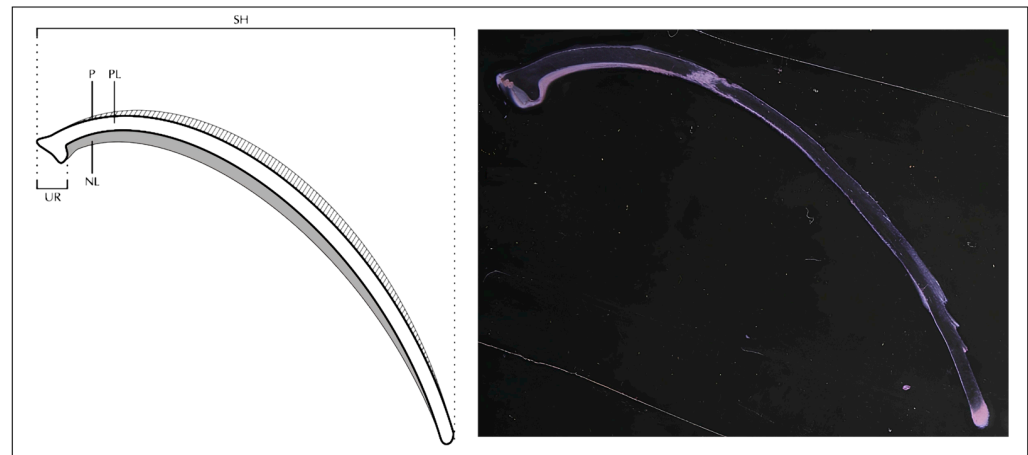


Figure 7. Cross-sectional stereomicroscope image and schematic illustration of a young *P. radiata* shell without visible annual growth lines (SH = 42.15 mm; UH = 1.372 mm). Abbreviations: P, periostracum; PL, prismatic layer; NL, nacreous layer; SH, shell height; UR, umbo region.

In contrast, older oysters exhibited clearly defined growth increments within the umbo region, allowing successive annual growth bands to be identified and counted (Figure 8). Specimens possessing three annual growth lines showed well-defined growth boundaries separating successive years of shell deposition, whereas older individuals exhibited up to five discernible annual increments. In some specimens, partial erosion and corrosion of the earliest growth lines were observed near the umbo region, although annual increments remained identifiable.

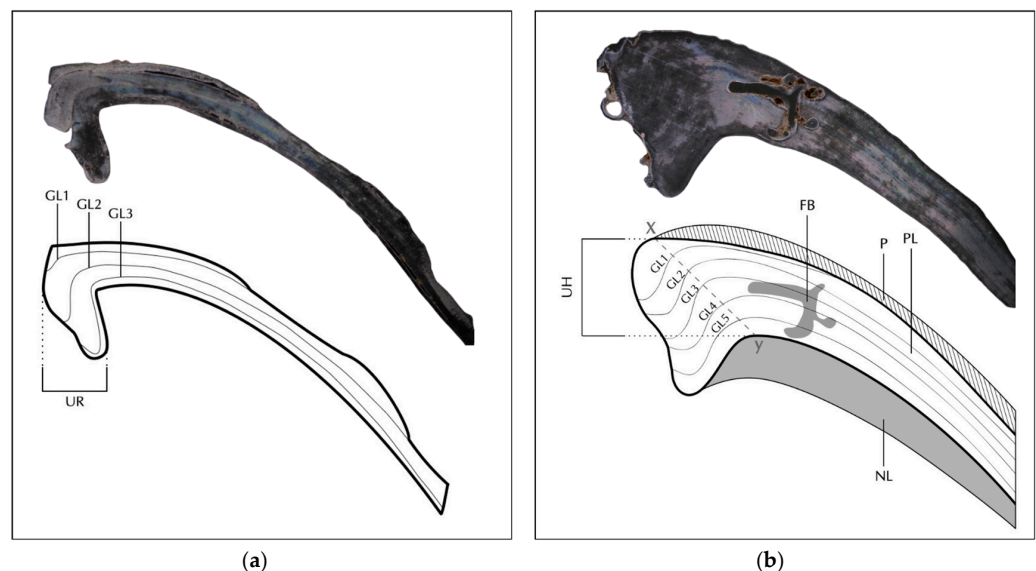


Figure 8. Cross-sectional stereomicroscope images and schematic illustrations of *P. radiata* shells showing annual growth-line identification in the umbo region. (a) Specimen with three visible growth lines (SH = 69.79 mm; UH = 3.8526 mm). (b) Specimen with five visible growth lines (SH = 87.3 mm; UH = 8.9441 mm) showing partial corrosion near the umbo. Growth lines are indicated as GL1–GL5. Abbreviations: P, periostracum; PL, prismatic layer; NL, nacreous layer; UH, umbo height; UR, umbo region; FB, foreign body.

3.5. Relationship Between Shell Height and Umbo Height

A strong positive relationship was observed between shell height (SH) and umbo height (UH), indicating that umbo growth closely reflected overall shell development (Figure 9).

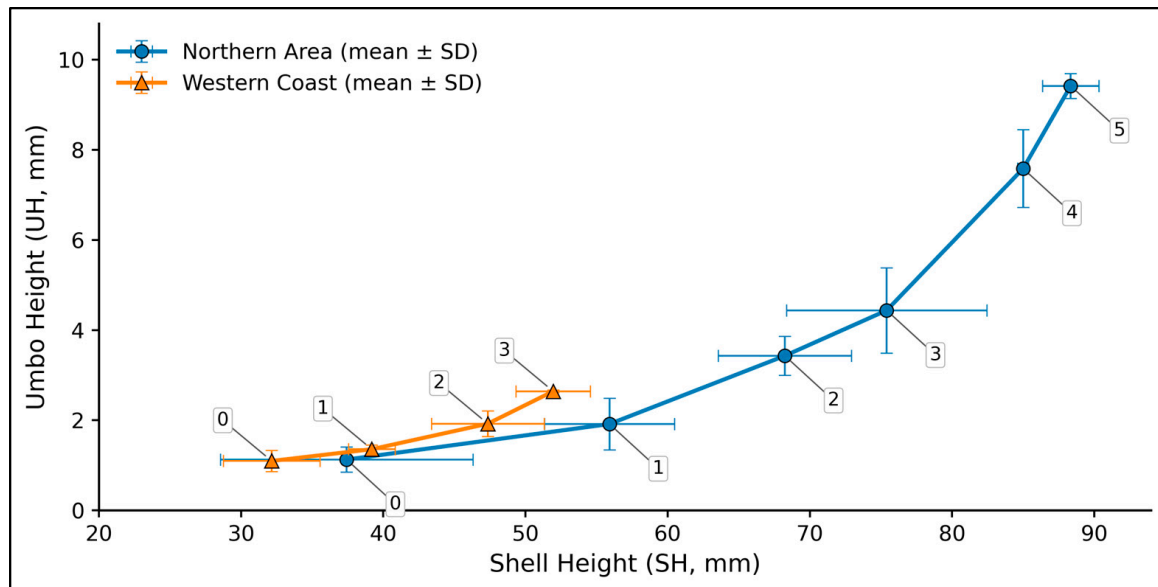


Figure 9. Observed morphometric growth patterns of shell height (SH) and umbo height (UH) across growth-line classes in the Northern Area and Western Coast populations. Points represent observed class means, error bars indicate $\pm$ SD for SH and UH, connecting lines show population-specific growth patterns, and numbers indicate annual growth-line classes.

This relationship enabled reconstruction of shell growth history from annual increments preserved within the umbo region and facilitated estimation of shell height corresponding to successive age classes. Observed SH–UH morphometric growth patterns across growth-line classes showed a close association between both shell dimensions in the Northern Area and Western Coast populations. Linear fits based on growth-line class means showed high coefficients of determination in the Northern Area ($R^2 = 0.842$) and the Western Coast ($R^2 = 0.925$). In both populations, increases in shell height were accompanied by corresponding increases in umbo height, although the Northern Area population exhibited a broader growth pattern and reached higher SH and UH values across successive growth-line classes.

3.6. Morphospace Analysis of Population Structure

Individual shell height and umbo height measurements revealed distinct morphometric patterns between the two pearl oyster populations (Figure 10). Linear regression and Pearson correlation analyses confirmed strong positive relationships between shell height and umbo height in both populations, with high correlation coefficients recorded for the Northern Area ($r = 0.8486$, $p < 0.001$) and the Western Coast ($r = 0.9043$, $p < 0.001$). These relationships indicate that umbo height scaled closely with shell height across the observed size range.

Northern Area individuals occupied a substantially broader morphospace and exhibited greater variability in shell and umbo dimensions. In contrast, Western Coast oysters were concentrated within a narrower morphometric space associated with smaller shell sizes and reduced umbo development. The 95% confidence ellipses further emphasized the broader morphometric dispersion of the Northern Area population relative to the more

restricted Western Coast population, indicating contrasting shell-growth patterns between the two habitats.

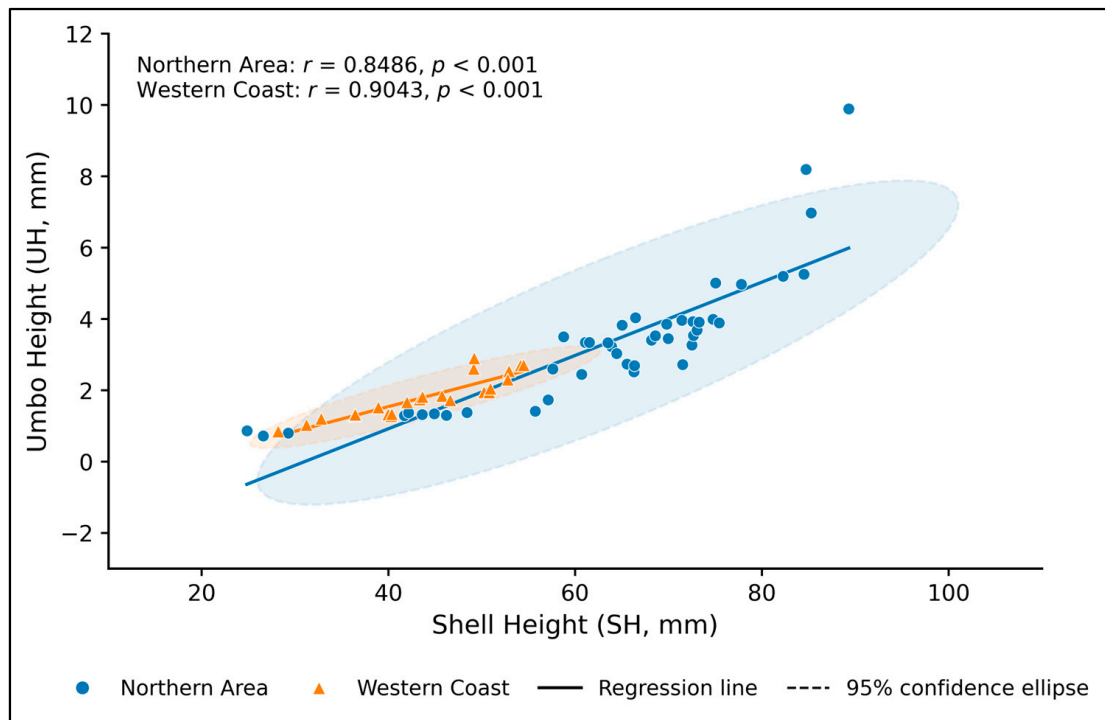


Figure 10. Scatter plot illustrating variation in shell height and umbo height among pearl oyster populations from the Northern Area and Western Coast of Bahrain. Solid lines represent fitted linear regression relationships, and dashed ellipses indicate 95% confidence ellipses based on the covariance structure of individual observations.

3.7. Age Structure and Growth-Line Counts

Growth-line counts revealed marked differences in age structure between populations inhabiting contrasting salinity regimes. Within the examined specimens, the Northern Area population exhibited a broader range of growth-line classes, extending from young individuals with no visible annual increments to oysters with five annual growth lines. In contrast, Western Coast oysters exhibited a more restricted age distribution within the examined sample, with the maximum observed count limited to three annual growth lines.

Mean shell height increased progressively with growth-line number in both populations. In the Northern Area population, mean shell height increased from 37.42 ± 8.88 mm in oysters without visible annual increments to 88.34 ± 1.98 mm in individuals possessing five growth lines. Corresponding umbo height increased from 1.1280 ± 0.277 mm to 9.4175 ± 0.276 mm across the same age range (Table S1).

In the Western Coast population, mean shell height increased from 32.15 ± 3.40 mm in oysters without visible annual increments to 51.95 ± 2.62 mm in individuals possessing three annual growth lines. Mean umbo height increased from 1.0970 ± 0.235 mm to 2.6430 ± 0.030 mm over the corresponding age classes. Within the examined samples, no Western Coast oysters possessing four or five annual growth increments were recorded.

Age-frequency distributions further highlighted differences between populations, with Northern Area oysters exhibiting a broader age structure extending to the 5–6 years age class, whereas Western Coast oysters were restricted to age classes up to 3–4 years (Figure S2).

3.8. Age-Related Growth Patterns

Growth curves reconstructed from annual growth increments revealed contrasting growth patterns between populations from the Northern Area and the Western Coast (Figure 11 and Table S1). In both populations, shell growth was most rapid during the early years of life and gradually declined with increasing age. However, Northern Area oysters attained larger shell dimensions and continued growth over a longer age range than Western Coast oysters.

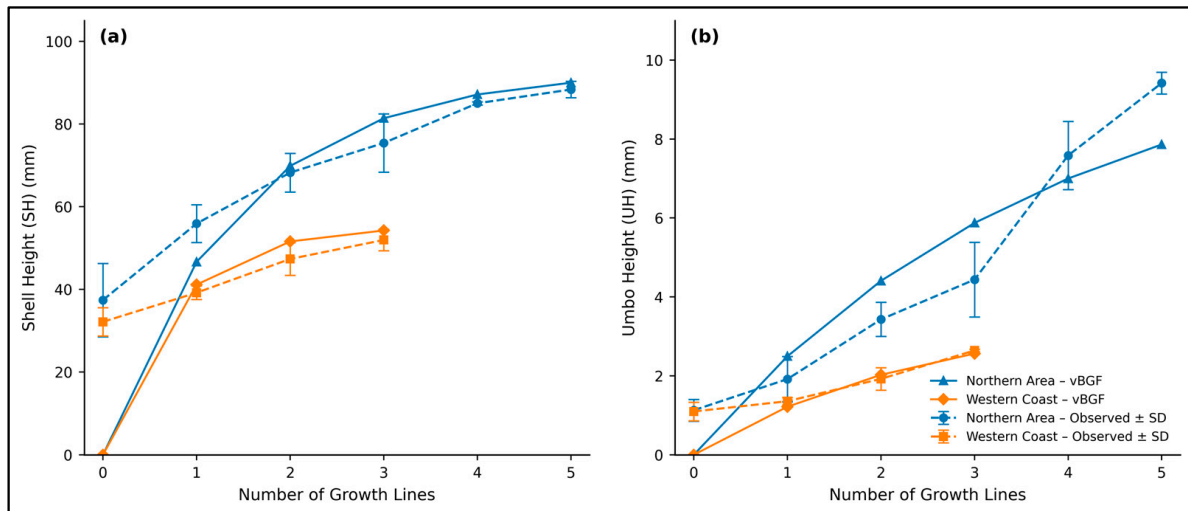


Figure 11. Comparative observed (mean $\pm$ SD) and von Bertalanffy Growth Function (vBGF) growth curves for (a) shell height (SH) and (b) umbo height (UH) across growth-line classes of *P. radiata* from the Northern Area (Hayr Bu Amamah) and Western Coast (Yasuf).

Observed shell height in Northern Area oysters increased from 37.42 mm in individuals lacking visible annual increments to 68.24 mm after two annual growth increments and exceeded 88 mm in individuals possessing five growth lines. Corresponding umbo height increased steadily from 1.13 mm to more than 9 mm during the same growth period.

Western Coast oysters exhibited a similar early growth pattern but attained substantially smaller shell dimensions. Mean shell height increased from 32.15 mm in oysters lacking visible annual increments to 51.95 mm in individuals possessing three annual growth increments, while mean umbo height increased from 1.10 mm to 2.64 mm. Within the examined samples, no individuals with more than three annual growth increments were recorded from the Western Coast population.

3.9. Von Bertalanffy Growth Model

Von Bertalanffy Growth Function analyses revealed clear differences in growth characteristics between populations inhabiting the two salinity regimes (Table 1). For shell height, the Northern Area population exhibited an asymptotic shell height (L_{∞}) of 92.80 mm and a growth coefficient (K) of 0.699. Corresponding umbo height parameters were $L_{\infty} = 10.70$ mm and $K = 0.265$.

In contrast, Western Coast oysters exhibited lower asymptotic dimensions despite higher growth coefficients. The estimated asymptotic shell height was 55.14 mm with $K = 1.371$, whereas asymptotic umbo height was 3.63 mm with $K = 0.407$. These model outputs indicate substantial differences in predicted asymptotic size and growth patterns between populations.

Table 1. Von Bertalanffy Growth Parameters for *P. radiata* in the Northern Area (Hayr Bu Amamah) and the Western Coast (Yasuf Island) Populations Based on Shell Height and Umbo Height.

Parameters ¹	Northern Area Growth Constants				Western Coast Growth Constants			
	<i>k</i>	<i>t</i> ₀	<i>L</i> _∞	RSS	<i>k</i>	<i>t</i> ₀	<i>L</i> _∞	RSS
Shell height SH (mm)	0.699	0	92.80	13,300.093	1.371	0	55.14	4540.18
Umbo height UH (mm)	0.265	0	10.70	62.506	0.407	0	3.63	5.9316

¹ Abbreviations: SH, shell height; UH, umbo height; *K*, growth coefficient; *t*₀, theoretical age at zero length; *L*_∞, asymptotic size; RSS, residual sum of squares.

Predicted growth curves generated by the von Bertalanffy model closely followed the observed age-specific shell height and umbo height measurements for both populations (Figure 11 and Table S1). Modelled shell height values for Northern Area oysters increased from 46.66 mm after one year to 89.98 mm after five years, whereas Western Coast oysters reached predicted shell heights of 41.15 mm, 51.59 mm, and 54.24 mm after one, two, and three years, respectively. Overall, both observed measurements and model predictions indicated that Northern Area oysters attained larger shell dimensions and spanned a broader age range than Western Coast oysters, reflecting distinct growth responses under contrasting salinity regimes.

3.10. Comparative Growth Responses Under Contrasting Salinity Regimes

Marked differences in growth characteristics were observed between *Pinctada radiata* populations inhabiting the Northern Area and the Western Coast (Figures 6 and 11; Table S1). The Northern Area population spanned a broader age range, attained larger shell dimensions, and exhibited greater umbo development than oysters from the Western Coast (Table 2). Individuals from the Northern Area reached shell heights of up to 88.34 ± 1.98 mm and exhibited up to five annual growth increments, whereas Western Coast oysters attained shell heights of up to 51.95 ± 2.62 mm and exhibited up to three annual growth increments.

Table 2. Comparative summary of age structure, shell morphometry, and environmental characteristics of the Northern Area and Western Coast populations in Bahrain waters.

Parameter ¹	Northern Area	Western Coast
Monthly salinity range (‰)	37–42	53–57
Oldest observed age class (years)	5–6	3–4
Mean SH of oldest age class (mm)	88.34	51.95
Mean UH of oldest age class (mm)	9.42	2.64
Shell thickness (mm)	3.81 ± 2.24 (0.79–10.68)	2.15 ± 0.71 (0.94–3.17)
SH vs. UH correlation (<i>r</i> , <i>p</i>)	0.8486, <i>p</i> < 0.001	0.9043, <i>p</i> < 0.001
Predicted asymptotic SH (vBGF) <i>L</i> _∞ (mm)	92.80	55.14
Predicted asymptotic UH (vBGF) <i>L</i> _∞ (mm)	10.70	3.63
Population characteristics	Broader age structure, larger shell dimensions, thicker shells, and greater umbo development	Restricted age structure, smaller shell dimensions, thinner shells, and reduced umbo development

¹ Abbreviations: SH, shell height; UH, umbo height; shell thickness values are presented as mean $\pm$ SD (min–max range); *r*, Pearson correlation coefficient; *p*, significance level; vBGF, von Bertalanffy Growth Function; *L*_∞, asymptotic size estimated from the growth model.

Differences between populations were also reflected in growth model outputs. Northern Area oysters exhibited substantially larger asymptotic shell height and umbo height values than Western Coast oysters, indicating greater predicted growth potential. In con-

trast, Western Coast oysters displayed higher growth coefficients but lower asymptotic dimensions, indicating rapid attainment of smaller adult sizes.

The contrasting growth responses coincided with persistent differences in environmental salinity between study areas. Monthly salinity records prior to specimen collection showed relatively stable salinity in the Northern Area (37–42‰), whereas the Western Coast remained persistently hypersaline, ranging from 53–57‰ during the same period (Figure 5). These environmental differences were associated with reduced shell dimensions, lower umbo growth, and a more restricted age structure in Western Coast populations compared with oysters from the Northern Area.

These findings demonstrate clear differences in age structure, shell development, and growth characteristics between *P. radiata* populations inhabiting contrasting salinity regimes in Bahrain waters.

4. Discussion

4.1. Validation of Growth Increments and Age Structure of *Pinctada radiata*

4.1.1. Annual Nature of Internal Growth Lines

The present study provides the first age and growth assessment of *P. radiata* populations in Bahrain waters based on internal shell growth-line analysis and confirms the suitability of annual shell growth lines for age determination and growth reconstruction. The acetate peel technique enabled clear visualization of growth lines within the prismatic middle shell layer, consistent with previous applications in pearl oysters [28,30], other marine bivalves [21], and broader sclerochronological studies [6,13]. This internal approach is particularly valuable because external shell surfaces in *Pinctada* sp. may be affected by taphonomic alteration [31], whereas internal shell layers are formed through biomineralization processes associated with prism and nacre deposition [32].

The regular spacing and continuity of growth increments observed in both populations support their interpretation as annual growth markers. Similar periodic increments have been documented in marine molluscs, including bivalves [21,33,34] and gastropods [35], and are widely applied for age determination and growth reconstruction [6,13]. Shell accretion responds to seasonal fluctuations in temperature, food availability, reproductive activity, and metabolic demand [10,11], which become preserved within shell structures as growth increments. In *Pinctada* species, annual growth increments and population-level biological variation have been reported from tropical and subtropical environments, including the Arabian Gulf [28,30] and other regions [36,37].

Seasonal environmental variability in Bahrain waters provides a plausible mechanism for annual increment formation. Seawater temperatures in the Arabian Gulf show pronounced annual cycles, with elevated summer temperatures and cooler winter conditions [14,25]. Such variability influences calcification, shell deposition [18], and biomineralization processes in pearl oysters and other marine bivalves [32]. Seasonal reductions in shell deposition during periods of environmental stress may produce distinct internal growth lines [10] that remain preserved within shell cross-sections and serve as chronological markers for age estimation [21,28].

External shell morphology alone was insufficient for reliable age reconstruction in *P. radiata*. External growth marks may be altered by erosion, bioerosion, taphonomic processes [31], encrustation, habitat disturbance, and shell surface modification [30]. Habitat-related shell variability in *P. radiata* [29,36] further limits the reliability of shell size or external features as age indicators. Internal growth-line analysis therefore provides more reliable chronological information for reconstructing age and growth history. The strong relationships between shell height and umbo height recorded in the Northern Area ($r = 0.8486$) and Western Coast ($r = 0.9043$) further support the age reconstruction approach

and are consistent with morphometric relationships reported in pearl oysters [29,36] and preserved shell structures [28,30].

4.1.2. Age Structure and Life Span

Age reconstruction revealed distinct population structures between the two study areas. Northern Area oysters included individuals up to approximately 5–6 years of age, whereas Western Coast oysters generally reached only 3–4 years. The broader age distribution in the Northern Area indicates the persistence of multiple age classes and survival of older individuals.

The observed age range of Northern Area oysters is consistent with previous reports for *P. radiata* and related pearl oysters from the Arabian Gulf and neighbouring regions, where individuals up to four to six years have been reported under warm subtropical conditions [28,37,38]. Similar variability in age structure among populations inhabiting different environmental settings [33,34] highlights the influence of local habitat conditions on demographic characteristics and population dynamics [30,37]. The coexistence of multiple age classes in the Northern Area suggests sustained recruitment and older-individual persistence [37,38], whereas the dominance of younger cohorts and shorter life span along the Western Coast reflects a more restricted age structure. These differences represent important life-history characteristics [39,40] and provide a basis for interpreting contrasting growth responses under different salinity regimes [20,37].

4.2. Growth Responses Under Contrasting Salinity Regimes

4.2.1. Shell Growth Patterns and Salinity-Associated Limitation

The most pronounced finding of this study was the substantial difference in growth characteristics between *P. radiata* populations inhabiting contrasting salinity regimes. Northern Area oysters attained larger shell dimensions and spanned a broader age range than Western Coast oysters. Shell heights reached up to 88 mm in the Northern Area, whereas Western Coast individuals generally reached up to 52 mm. Von Bertalanffy modelling similarly predicted a higher asymptotic shell height in the Northern Area population (92.80 mm) than in the Western Coast population (55.14 mm).

These differences indicate distinct growth patterns within the same regional marine system. Northern Area oysters showed sustained shell deposition over a longer period, whereas Western Coast oysters approached asymptotic size at younger ages and smaller shell dimensions. The higher growth coefficient estimated for Western Coast oysters indicates a more rapid approach to asymptotic size, but not a larger ultimate shell size. Comparable growth dynamics occur in bivalves [4,5], where environmental conditions can produce contrasting combinations of growth rate and asymptotic size [36,39,40].

Differences were also evident in umbo development and overall growth performance. Northern Area oysters exhibited greater umbo height and continued shell deposition across successive age classes, whereas Western Coast oysters showed reduced umbo growth and fewer age classes. Because the umbo region preserves cumulative records of shell accretion throughout life [21,28], these differences indicate long-term divergence in shell development between habitats.

The salinity contrast between study areas persisted throughout the annual cycle, with 37–42‰ in the Northern Area compared with 53–57‰ on the Western Coast. Salinity is a major environmental factor influencing shell formation and growth in marine bivalves [17]. Elevated salinity can alter ionic regulation [19,41], modify biomineralization processes [18,32], and increase maintenance costs associated with osmotic balance [20,42]. Experimental studies on pearl oysters and other marine bivalves show that growth performance commonly declines when salinity deviates from species-specific optima [17,18,41].

The smaller shell dimensions, reduced umbo growth, thinner shells, and shorter life span of Western Coast oysters are consistent with salinity-associated growth limitation and a dwarf-like growth pattern under persistent hypersalinity. Although multiple factors may influence growth in natural populations, the consistency of the observed patterns suggests that long-term exposure to elevated salinity appears to be an important factor influencing shell development and asymptotic shell size in western Bahrain populations of *P. radiata* [41,43]. Greater shell thickness in Northern Area oysters is consistent with enhanced shell accretion and prolonged growth under lower salinity conditions [18,32].

4.2.2. Energy Allocation and Life-History Characteristics

The observed growth differences may reflect contrasting energy-allocation strategies under different environmental conditions. In marine bivalves, available energy is partitioned among maintenance, shell formation, growth, reproduction, and other metabolic processes [20]. Conditions that increase maintenance requirements can reduce energy available for somatic growth [17,19], resulting in smaller adult size and altered growth trajectories [18,36].

Although *P. radiata* is recognized as a euryhaline pearl oyster species capable of tolerating broad environmental conditions [37,38], prolonged exposure to elevated salinity may influence growth performance and shell development [41,43]. Western Coast oysters exhibited relatively rapid early growth, smaller asymptotic shell size, and shorter life span compared with the Northern Area population. This pattern is consistent with a growth response in which individuals approach asymptotic size over a shorter period while remaining smaller than conspecifics in more moderate salinity conditions.

The progressive decline in annual growth increment width with increasing age reflects the typical bivalve growth pattern [4,5]. Similar rapid early growth of *P. radiata* spat and yearlings has also been reported from Bahrain waters [44]. Early stages are characterized by rapid shell accretion and expansion, whereas growth rates decline as energy allocation shifts toward maintenance and reproduction [20,39]. The earlier attainment of growth asymptotes in Western Coast oysters therefore indicates a more constrained developmental trajectory relative to the Northern Area population. Increased energetic expenditure associated with osmotic regulation under salinity stress may alter energy allocation patterns and ultimately affect growth performance [45]. Similar life-history patterns occur in marine invertebrates exposed to environmentally restrictive habitats [39,40], where reduced adult size and truncated age structures may occur despite recruitment and population persistence [37,38].

Taken together, age structure, shell dimensions, umbo development, shell thickness, and growth model outputs indicate that environmental variability can strongly influence growth dynamics and life-history characteristics of *P. radiata*. Salinity is a key distinction between the two examined populations; however, it should not be interpreted in isolation, as pearl oysters may also respond to associated differences in water chemistry, food availability, hydrodynamics, sediment characteristics, and reproductive investment. Salinity should therefore be viewed as part of a broader habitat-related gradient that may influence physiological performance and energy allocation in filter-feeding bivalves [17,20].

4.3. Population Divergence Across Salinity Habitats

4.3.1. Evidence of Phenotypic Divergence

The marked differences in shell size, age structure, umbo development, and growth characteristics indicate substantial phenotypic divergence across habitats. Despite belonging to the same species and occurring within the same regional marine system, Northern Area and Western Coast oysters exhibited consistently different growth outcomes.

Phenotypic variation among marine bivalve populations is common [46] and often reflects the combined influence of environmental conditions and population-specific biological characteristics [36,38]. In pearl oysters, differences in shell morphology [29,36], growth rate and population structure [37,38], and other biological traits have been reported across environmental gradients and regional habitats [20,46]. The present findings add to this evidence by demonstrating clear differences in age structure and growth responses between populations inhabiting contrasting salinity regimes in Bahrain waters.

Such variation is consistent with genotype-by-environment interaction [47], whereby environmental conditions influence growth-related traits and contribute to population-level variation in morphology and life-history characteristics. Although genetic analyses were beyond the scope of the present study, the reduced shell size of Western Coast oysters may represent part of a broader salinity-associated phenotypic gradient in Bahrain waters, consistent with shell-shape plasticity under contrasting natural environments [46] and salinity tolerance reported in *Pinctada imbricata radiata* [41]. This pattern may reflect phenotypic plasticity and possible local adaptation to persistent hypersaline conditions, highlighting the importance of future population genetic and transcriptomic analyses to determine whether the Western Coast population represents an environmentally induced morphotype or a distinct strain of *P. radiata* [43,48].

4.3.2. Perspectives from Recent Molecular Studies

Recent molecular investigations of pearl oysters and other marine bivalves show that populations inhabiting environmentally stressful habitats may exhibit distinct metabolic and transcriptomic signatures associated with energy metabolism [20,42,45], osmotic regulation [19,41–45,48], biomineralization [32,49,50], oxidative balance, and cellular stress regulation [43,49]. Differential expression of genes involved in shell formation [49,50] and stress-response pathways has also been reported under salinity, temperature, and other environmental stressors [41,43,49].

The pronounced differences in shell growth, shell dimensions, shell thickness, and life span between Northern Area and Western Coast oysters suggest that salinity influences biological processes linked to growth and shell development. The observed responses under the persistent hypersaline conditions recorded along the Western Coast are consistent with evidence that salinity stress can affect osmoregulatory responses [41,42] and transcriptomic regulation in pearl oysters [43], while environmental stressors may influence biomineralization pathways [32,49,50] and energy allocation [20,42,45]. Future studies integrating shell growth-line analyses with physiological and molecular approaches may clarify mechanisms controlling growth variation and salinity tolerance in *P. radiata* pearl oysters.

4.4. Ecological Implications

This study demonstrates that substantial variation in age structure, life span, and growth characteristics can occur within *P. radiata* populations inhabiting different habitats in Bahrain waters. Older and larger individuals in the Northern Area suggest greater potential for maintaining mature breeding stocks and long-term population stability, whereas younger individuals and smaller shell size along the Western Coast indicate a more restricted demographic structure.

Population age composition is ecologically important because it influences reproductive output, recruitment potential, and resilience to environmental disturbance [51,52]. Larger and older bivalves generally contribute disproportionately to reproductive capacity through higher gamete production [52] and extended spawning participation [51].

Habitat-related differences in age structure may therefore have important implications for population dynamics and long-term persistence [37,38].

The findings also highlight the value of shell growth-line analyses for understanding demographic processes in pearl oyster populations. Age-based assessments provide information that cannot be obtained from shell size alone [21,28] and improve interpretations of population structure, growth variability, and habitat-related differences [30,37]. Such information is relevant for conservation and monitoring programmes, where age-class distribution can support evaluation of population condition and recruitment success.

More broadly, the present study contributes to evidence that environmental gradients can influence marine bivalve populations across relatively small geographic scales [36,38]. Understanding habitat-related growth variation is therefore important for interpreting population responses to environmental variability and developing ecologically informed management strategies for pearl oyster resources in Bahrain waters and the wider Arabian Gulf [37,38]. The morphometric and growth differences observed between populations were consistent across shell size, umbo development, shell thickness, age structure, and growth-model outputs. Nevertheless, as the two populations occur under naturally contrasting habitat conditions, these differences are interpreted as being associated with the overall habitat gradient, with persistent hypersalinity representing the main environmental contrast. Future studies incorporating broader spatial sampling and independent growth-line validation would further strengthen this interpretation.

5. Conclusions

This study presents the first age and growth assessment of the pearl oyster *Pinctada radiata* in Bahrain waters based on internal shell growth-line analysis and provides the first age-based comparison of populations inhabiting contrasting salinity regimes within Bahrain waters. Internal growth increments preserved within the prismatic middle shell layer provided a reliable basis for age determination and growth reconstruction using acetate peel techniques and von Bertalanffy growth modelling.

Distinct differences in age structure and growth responses were observed between populations. Northern Area oysters attained larger shell dimensions, exhibited broader age distributions, and included individuals up to approximately 5–6 years of age, whereas Western Coast oysters displayed smaller shell dimensions, a more restricted age structure, and generally reached 3–4 years of age. Von Bertalanffy growth analyses predicted asymptotic shell heights of 92.80 mm and 55.14 mm for the Northern Area and Western Coast populations, respectively.

The observed differences in age structure, shell growth, umbo development, and life span were associated with contrasting salinity regimes between study areas. Persistent hypersaline conditions along the Western Coast were associated with reduced growth potential, smaller adult size, restricted age structure, and shorter life span relative to populations inhabiting the lower-salinity Northern Area.

Overall, this study establishes the first sclerochronology-based framework for evaluating age structure and growth responses of *P. radiata* in Bahrain waters and provides new insights into population variation under contrasting salinity regimes in the Arabian Gulf. The findings highlight the importance of environmental heterogeneity in shaping pearl oyster population characteristics and provide a foundation for future ecological monitoring, population assessments, and conservation-oriented management of pearl oyster resources in the region.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/jmse14131186/s1>, Figure S1: Comparative shell height (SH) size-frequency distribution of *P. radiata*; Figure S2: Comparative age-class frequency distribution of *P. radiata*; Table S1: Observed and vBGF-predicted shell height (SH) and umbo height (UH) values across growth-line classes of *P. radiata* populations.

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