Indian J. Fish., 70(1): 10-17, 2023
DOI: 10.21077/ijf.2023.70.1.83950-02

Morphological trends in three different populations of the noble scallop *Mimachlamys crassicostata* (G. B. Sowerby II, 1842) along the South China Sea Coast and their relationship to environmental factors

JIAQI SU[1,2,3], BAOSUO LIU[1,2,3] AND CHANGBO ZHU[1,2,3]
[1]*South China Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences, Guangzhou - 510 300, P. R. China*
[2]*Key Laboratory of South China Sea Fishery Resources Exploitation and Utilisation, Ministry of Agriculture and Rural Affairs, Guangzhou - 510 300, P. R. China*
[3]*Guangdong Provincial Key Lab, Fishery Ecology and Environment, Guangzhou - 510 300, P. R. China*
e-mail: changbo@scsfri.ac.cn

ABSTRACT

This study was carried out to assess the spatial patterns of morphological characteristics of the three cultured populations of the scallop *Mimachlamys crassicostata* (G. B. Sowerby II, 1842), from Yazhou Bay, Liusha Bay and Mirs Bay along the South China Sea coast and to determine whether any of the morphological characteristics could be related to selected environmental parameters. Morphological ratios of seven traits were analysed by classification and regression tree to evaluate the morphological variations in 1353 samples from three geographic locations. In addition, relationships between discriminatory morphological characteristics (ratios of shell weight to length, shell weight to height, whole weight to length and shell weight to adductor muscle weight) and nine environmental parameters (seawater temperature, salinity, pH, chemical oxygen demand, dissolved inorganic nitrogen, active phosphate, total petroleum hydrocarbons, dissolved oxygen (DO) and chlorophyll a were assessed using mixed-effects linear models (LMMs). Results showed that more than 80% of individuals could be assigned to their collection locations based on the classification and regression tree. The accuracy of assigning individuals to their collection location of Mirs Bay, Yazhou Bay and Liusha Bay based on morphological variation was 85.52, 80.30 and 80.68%, respectively. Results of the LMMs revealed that ratios of shell weight to height and whole weight to length correlated positively with temperature and salinity, respectively. Shell weight to adductor muscle weight correlated negatively with DO concentration, indicating that high DO levels may be necessary to provide a suitable environment for scallops cultured in a food-rich coastal bay. These results may be helpful for future resource management, including stock recognition, productive management and stock conservation of *M. crassicostata* in the South China Sea.

Keywords: Cultured population, Environmental parameters, Mixed-effects linear model, Morphological characteristics, Stock conservation

Introduction

Morphological characters are visual and convenient tools to infer taxonomic affinities and have been used to distinguish different populations, subspecies and species in bivalves (Wang *et al*., 2004; Lomovasky *et al*., 2008; Sigwart, 2009). As phenotypic trait can be altered by genetic variation and environmental factors, morphological traits always have genetic correlations with other economic phenotypic traits such as body weight (Luo *et al*., 2013; Zhao *et al*., 2014; Marie-Orleach *et al*., 2017). Thus, morphological traits are useful indices for assessing the growth state of molluscs (Marquez *et al*., 2010; Epelbaum *et al*., 2011).

Shell morphology is likely to affect locomotion performance and self-protection ability, while the phenotypic plasticity could enhance the adaptability of molluscs to their environment (Peyer *et al*., 2011; Tremblay and Guderley, 2012). Phenotypic plasticity of shell morphology could allow molluscs to respond to different selective pressures caused by environmental conditions, including depth of distribution, water movement, type of sediment, food quantity and contaminants (Peyer *et al*., 2010; Selin, 2013). Thus, analyses focused on identifying similarities and differences in morphological variation and inferring mechanisms involved in generating morphological diversity which could improve taxonomic identification, germplasm conservation and fisheries management of bivalves.

The noble scallop *Mimachlamys crassicostata* (G. B. Sowerby II, 1842), which is distributed from the lower edge of the intertidal zone to a depth of about 300 m, is found mainly in the coastal waters of Honshu, Shikoku and Kyushu in Japan, Thailand, Indonesia and the South China Sea. Since 1980s, *M. crassicostata* has been considered as an economically important species in the bivalve aquaculture industry along the south coast of

China due to its rapid growth and short culture period. It is typically cultured at 2-7 m depth in Fujian, Guangdong and Hainan Provinces (Lu *et al.*, 2017). The broodstock selected from hatchery-cultured stock have been used to produce the next cultured generation every year for decades and this could cause low effective population size and inbreeding. Yuan *et al.* (2009) reported that the genetic composition of cultured *M. crassicostata* populations in southern China presented low degree of variation and significant geographic structure among regions. Therefore, effective germplasm and aquaculture management strategies are needed for *M. crassicostata*. Previous studies of *M. crassicostata* have focused mainly on toxicology, shell colour inheritance, genetic markers, gene expression and genetic diversity (Pan and Wang, 2008; Wang *et al*., 2013; Zheng *et al*., 2013; Lu *et al*., 2016). Studies of morphological variations in *M. crassicostata* and their responses to environmental factors are lacking.

The goals of this study were to determine whether spatial patterns exist in the morphological characteristics of three *M. crassicostata* populations along the South China Sea coast and whether any of the morphological characteristics could be related to selected environmental parameters. The results of this research will be useful for germplasm management and optimising the distribution of *M. crassicostata* stock based on environmental monitoring.

Materials and methods

Sample collection and analysis

Samples of 1-year old *M. crassicostata* were collected separately from each of three cultured populations located in Yazhou Bay (SY), Liusha Bay (LZ) and Mirs Bay (SZ) (468, 472 and 463 individuals respectively), in the South China Sea, during May 2016 to June 2016 (Fig. 1). Offsprings of the cultured populations were hatched in a local nursery farm. Spats (over 0.5 cm shell length) were transferred to the sea and cultured in lantern net on suspended longlines until harvested. Samples from SY and LZ were transported live in cool moist conditions to the Tropical Fisheries Research and Development Center, South China Sea Fisheries Research Institute, Hainan Province, P. R. China. Samples from SZ were transported in the same way to Shenzhen Base of the South China Sea Fisheries Research Institute, Guangdong Province, P. R. China. Scallops were first cleaned to remove attached organisms. Dead, broken or malformed individuals were abandoned. Then the samples were washed thoroughly in fresh filtered seawater before taking measurements. Finally, morphological ratios of seven traits were analysed by classification and regression tree to evaluate the morphological variations in 1353 samples from three geographic locations (Table 1). Shell length (L), hinge length (HL), shell height (H) and shell width (W) were measured using digital vernier calipers (Liansi Shenzhen, China) to the nearest 0.01 mm. The whole weight (WW), shell weight (SW) and adductor muscle weight (AW) were measured using an electronic balance (Yuheng Shenzhen, China) to the nearest 0.01 g.

Seasonal (May 2015, August 2015, November 2015 and March 2016) environmental data were collected at the three sites (Table 2). The average values of nine environmental parameters *viz*., seawater temperature, salinity, pH, chemical oxygen demand, dissolved inorganic nitrogen, active phosphate, total petroleum hydrocarbons, dissolved oxygen (DO) and Chlorophyll 'a', were used to assess their potential influence on *M. crassicostata* morphological characteristics. Environmental data for Liusha Bay were based on water sample testing conducted once per season. Dissolved oxygen, salinity, pH and temperature were measured *in situ* using a YSI 556 device (Yellow Springs, OH, USA). Dissolved inorganic nitrogen, active phosphate concentrations, total petroleum hydrocarbons, chemical oxygen demand and Chlorophyll 'a' in seawater samples were analysed according to the methods in the Specification of Oceanographic Survey GB17378.4-2007 (SBQTS, 2007). Environmental conditions data for Yazhou Bay and Mirs Bay were based on water quality monitoring information data in the sea areas of Sanya and Shenzhen from the website of China's State Oceanic Administration (http://www.soa.gov.cn/zwgk/hyhjxx/) to represent conditions at Mirs Bay and Yazhou Bay, respectively.

Statistical analysis

Statistical analyses of the data included: Generating a classification and regression tree (CART) to match

Fig. 1. Map showing the study area and location of sampling sites

Table 1. Morphometric characteristics of Liusha Bay (LZ); Mirs Bay (SZ) and Yazhou Bay (SY) populations (n = 1353)

Morphometric characteristics	LZ	SZ	SY
Shell length (mm)	59.37-81.74	60.86-81.81	59.84-77.44
Shell height (mm)	44.41-78.59	65.34-84.22	62.81-82.2
Shell width (mm)	17.84-31.84	18.39-28.15	19.15-34.8
Hinge length (mm)	33.01-50.72	35.14-51.88	35.55-49.95
Shell weight (g)	18.56-36.25	18.31-36.71	21.99-40.81
Adductor muscle weight (g)	2.41-8.17	2.81-9.52	3.09-8.04
Whole weight (g)	28.31-55.66	28.72-73.92	34.19-69.5

Table 2. Environmental parameters recorded in Mirs Bay, Liusha Bay and Yazhou Bay during May 2015 to March 2016

Environmental parameters	Mirs Bay	Liusha Bay	Yazhou Bay
Dissolved inorganic nitrogen (mg l^{-1})	0.24±0.10	0.52±0.78	0.034±0.026
Active phosphate (mg l^{-1})	0.016±0.013	0.012±0.006	0.003±0.002
Total petroleum hydrocarbons (mg l^{-1})	0.062±0.043	0.026±0.011	0.016±0.003
Chemical oxygen demand (mg l^{-1})	1.78±1.40	2.77±1.34	0.505±0.266
Dissolved oxygen (mg l^{-1})	7.06±1.54	6.54±1.40	6.57±0.301
pH	8.28±0.08	8.46±0.09	8.13±0.06
Chlorophyll a (mg l^{-1})	2.61±1.28	3.18±2.57	2.43±1.65
Temperature (℃)	22.69±6.35	26.63±6.14	27.85±2.26
Salinity (ppt)	2.73±0.55	31.04±1.65	32.75±0.54

individuals to their original sites and to quantify the importance of the biometric variables; Creating a description of the biometric variables selected in step one and using mixed-effects linear models (LMMs) to highlight the relationships between biometry and environmental parameters.

In step one, 21 biometric variables (SW/AW, SW/WW, SW/L, SW/H, SW/W, SW/HL, AW/WW, AW/L, AW/H, AW/W, AW/HL, WW/L, WW/H, WW/W, WW/HL, L/H, L/W, L/HL, H/W, H/HL, W/HL) for 300 random individuals from each cultured population were used to build a classification tree (Fig. 2). After pruning, the numbers and biometric variables of the remaining 151 individuals in each cultured population were used to validate the classification tree by checking to see if the output of the tree matched individuals to their collection locations. In step two, the morphological ratios identified as the most discriminatory by the previous classification method were analysed using Kruskal-Wallis statistics to test for spatial differences. In step three, LMMs were used to quantify the relationships between certain morphological traits and environmental factors.

In order to test the performances of the classification and regression tree (CART), the accuracy rate was used. It was determined using the relation:

$$\text{Accuracy rate} = T_i / (T_i+F_i) \times 100\%$$

where Ti is the number of individuals that are correctly classified to site i and F_i is the numbers of individuals that are erroneously classified to site i.

Statistical analysis was performed following the method described by Caill-Milly *et al.* (2014). Calculations were carried out using R Software (RCore Team, 2013) and Rpart was used to generate the classification tree

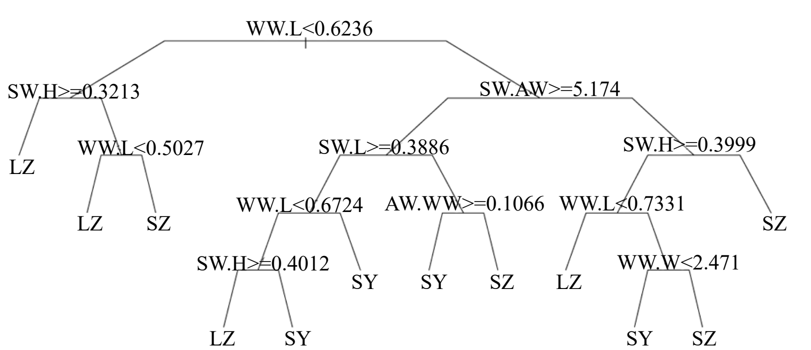

Fig. 2. Plot of the selected classification tree obtained before pruning; LZ: Liusha Bay; SY: Yazhou Bay; SZ: Mirs Bay

(Therneau *et al*., 2013). Linear mixed-effects models were generated using the lmer procedure from the lmerTest library (Kuznetsova *et al*., 2015) and the nlme library (Pinheiro *et al*., 2014).

Results and discussion

Twenty-one biometric variables were used to build a classification tree to assess the morphological variations in different geographic populations of *M. crassicostata*. The selected classification tree and the verification matrix are shown in Fig. 3 and Table 3, respectively. Shell valves from LZ were differentiated from those from SZ and SY by a low WW/L ratio (<0.6236) and were then differentiated from the other individuals from SZ by a high SW/H ratio (≥0.3213). Individuals from SY were differentiated from those from SZ by three morphological characteristics; some individuals from SY had a high WW/L ratio (>0.6236), and the others were characterised by a SW/AW value >5.174 or a SW/L value >0.3886. The accuracy of assigning individuals to their collection location of SZ, SY and LZ based on morphological variation was 85.52, 80.30 and 80.68%, respectively. Compared to linear discriminant analysis, classification and regression trees (CARTs) do not depend on data fitting, covariance homogeneity, or normality conditions (Feldesman, 2002). Furthermore, CART has been previously used to quantify the importance of the target variable and to investigate interactions between predictors in sub datasets (Kail *et al*., 2015). Research suggests that CART can successfully select and identify more significant parameters for predicting distribution or habitat of clam and abalone (Kock and Wolmarans, 2007; Lessard and Campbell, 2007). In the current study, WW/L, SW/L, SW/H and SW/AW were the variables that were most significant in separating and identifying individuals from different populations. In fact, there are few studies that focus on the scallop hinge. The hinge ligament has received more attention than the hinge itself because it is involved in the hydrodynamics and movement behaviour of scallops (Cheng and Demont, 1996; Tremblay, *et al*., 2012). However, hinge length was less applicable for distinguishing individuals from different populations.

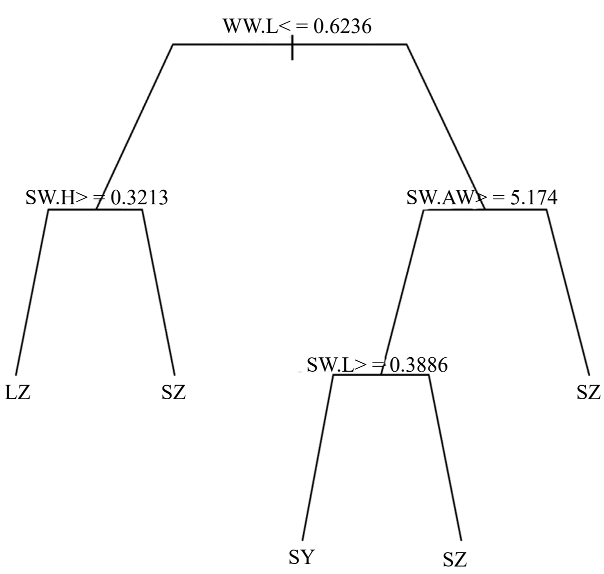

Fig. 3. Plot of the selected classification tree obtained after pruning; LZ, Liusha Bay; SY, Yazhou Bay; SZ, Mirs Bay

Table 3. Verification matrix related to the pruned classification tree in Fig. 3

Real/Predicted	SZ	SY	LZ	Accuracy rate %
SZ	124	19	8	85.52
SY	19	106	26	80.30
LZ	2	7	142	80.68

Table 4 shows the SW/AW, SW/L, SW/H and WW/L data for the three populations. SY had the highest values of SW/L, SW/H and WW/L, among the three populations, which were 0.43±0.04, 0.40±0.03 and 0.73±0.07 respectively. The SW/L and SW/H ratios of the LZ population were greater than those of the SZ population. They were 0.37±0.04 and 0.39±0.05 respectively. The WW/L value in the SZ population fell in between those of the SY and LZ populations. The SZ population had the lowest SW/L and SW/AW ratios among the three populations. The SW/AW ratio of LZ was 5.98±0.96 which was higher than SY (5.87±0.75). Kruskal-Wallis tests applied to each ratio confirmed significant differences among sites.

Morphological variations are widespread among different geographic populations of molluscs. Thus, knowledge about specific shellfish morphological variations could be applied to stock assessment and management (Lomovasky *et al.*, 2008; Owada *et al.*, 2013; Guo *et al*., 2017). The adductor muscle is the most valuable edible part of the scallop and it is the most important locomotory organ in scallops, as it is used for swimming and defense. High shell mass can influence the gravitational effect on scallops and potentially reduce movement ability (Tremblay *et al*., 2017). Thus, a high SW/AW ratio may mean low commercial value and poor swimming ability of scallops.

Results of the mixed-effects linear models revealed significant positive correlations between SW/H and temperature and WW/L and salinity and a negative correlation between SW/AW and DO concentration (Table 5). No environmental factor was linked with SW/L. Previous reports (Laing, 2002; Hiebentha *et al*., 2012) indicate that both temperature and salinity can influence the growth and shell formation of shellfish, which suggests that temperature and salinity may affect the morphological ratios of scallops. Telesca *et al.*

Table 4. Morphological characteristics of SZ, SY and LZ populations (n = 1353)

Indicators	SZ	SY	LZ	Range	Chi-square value	p value
SW/AW	4.79±0.79	5.87±0.75	5.98±0.96	3.95-8.20	408.71	1.78E-89
SW/L	0.37±0.04	0.43±0.04	0.37±0.04	0.27-0.53	451.61	8.58E-99
SW/H	0.35±0.04	0.40±0.03	0.39±0.05	0.26-0.56	333.31	4.21E-73
WW/L	0.71±0.09	0.73±0.07	0.57±0.07	0.38-0.98	650.11	6.76E-142

Table 5. Linear multilevel models showing the effect of environmental parameters on morphological characteristics identified for the scallop populations using classification trees

Morphological ratios	Null model		Final model	
	Intraclass correlation coefficient (%)	Significance between null model containing a random spatial effect and one without	Significant environmental variables	p-value of fixed effects
SW/L	41.97	< 0.0001	–	–
SW/H	30.91	< 0.0001	Temperature	0.027
WW/L	54.01	< 0.0001	Salinity	0.0435
SW/AW	38.00	< 0.0001	DO	0.002

(2018) suggested that salinity has the strongest effect on the spatial patterns of shell shape variation of North Atlantic and Arctic blue mussels (*Mytilus edulis* and *M. trossulus*), while temperature and food supply are the main drivers of shape heterogeneity. Furthermore, mussels showed similar shell shape responses to less favourable environmental conditions, with the formation of elongated, narrow shells. Tomiyama (2021) observed that clams (*Ruditapes philippinarum*) originating from unsuitable habitats to suitable habitats showed a reduction in shell height relative to shell length, while clams from suitable habitats to unsuitable habitats showed a greater growth in shell height than shell length. Our results show that cultured population in Leizhou had the lowest WW/L ratio. The noble scallop *M. crassicostata* is a stenohaline marine bivalve mollusc with an optimum salinity range for growth of 28 to 32 ppt (Tan *et al.,* 2022). Liusha Bay had the lowest annual average salinity (31.04±1.65 ppt) compared to Mirs Bay (32.73±0.55 ppt) and Yazhou Bay (32.75±0.54 ppt). Suitable salinity in Liusha Bay may lead to a greater contribution of shell length to the growth (whole weight) of the scallop. Cultured population in Yazhou Bay had both the highest SW/H and SW/L ratio, which reflects higher thickness or weight of scallop shell. Some of the differences in shell thickness can be explained by temperature. Lagos *et al.* (2021) observed that overall higher shell density was recorded in scallop *Argopecten purpuratus* exposed to increased elevated temperature rarely occurring in Tongoy Bay. A positive correlation between shell thickness and site temperature was reported in eastern oyster (*Crassostrea virginica*) along the eastern North American seaboard ranging from New Brunswick, Canada, to Florida (Lord and Whitlatch, 2014).

Dissolved inorganic nitrogen, COD and active phosphate are commonly used indicators to assess water quality or eutrophication (Liu *et al.,* 2011). As suspension feeders consume more organic matter from increasing abundance of phytoplankton, their rate of growth should also increase if they are food limited (Wall *et al.,* 2013). The net effect of eutrophication on bivalves, therefore, depends on the balance between enhanced food supply and habitat alterations that are mediated by attributes of the receiving estuary and differences among species, particularly feeding habits, feeding physiology and tolerance to hypoxia (Carmichael *et al.,* 2012). Although good trophic conditions are expected to lead to better growth, results of this study suggest that no morphological ratio was correlated with the concentration of Chlorophyll 'a', dissolved inorganic nitrogen, COD and active phosphate. This may be because trophic conditions were good in all three bays from which the scallops were collected. Due to land runoff, or the aquaculture environment, plankton and organic matter were abundant for scallops in the three study areas (Si *et al.*, 2013; Li *et al.*, 2014). Our results demonstrated that a higher DO level might result in a higher AW/SW ratio, which indicates high commercial value and swimming ability of scallops. Dissolved oxygen is known to affect metabolism and eventually lead to growth and survival in marine invertebrates. For the scallop *C. farreri*, a low DO level reduced the survival rate and decreased immunity (Chen *et al.*, 2007; Yu, *et al.*, 2010). Furthermore, a high DO concentration is always related to good water exchange and water quality (Oldham *et al.*, 2017; Kakehi, *et al.*, 2018). Therefore, a high DO level may be necessary for a suitable environment for scallop culture in a food-rich coastal bay. However, morphological traits can be altered by genes and further verification of the genotype-environment interaction is needed.

In this study, variations in morphological patterns could be applied for stock classification of different *M. crassicostata* populations, as >80% of individuals could be assigned to their collection locations based on these variations. Thus, the CART was an effective tool for discriminating *M. crassicostata* cultured in the three different sites. The morphological ratios such as SW/AW, SW/L, SW/H and WW/L differed significantly among the different populations. In addition, SW/H, WW/L and SW/AW values showed a significant relationship with seawater temperature, salinity and DO concentration, respectively. Mixed-effects linear models results indicated that DO may be a key factor in culture management of *M. crassicostata*. These results provide valuable information about population identification of *M. crassicostata* in the South China Sea, which may be helpful in taxonomic identification, stock conservation and fisheries management of scallops.

Acknowledgements

This project was funded by Shandong Key Laboratory of Marine Ecological Restoration (Grant No: 201917), Guangdong Pearl Industry Development Project (Z2015013) and Central Public-interest Scientific Institution Basal Research Fund, SCFSRI (2015TS27). Authors are grateful to all the laboratory staff for the technical support.

References

Caill-Milly, N., Bru, N., Barranger, M., Gallon, L. and D'Amico, F. 2014. Morphological trends of four manila clam populations (*Venerupis philippinarum*) on the French Atlantic Coast: Identified spatial patterns and their relationship to environmental variability. *J. Shellfish Res.*, 33: 355-372. DOI:10.2983/035.033.0205.

Carmichael, R. H., Shriver A., C. and Valiela, I. 2012. Bivalve response to estuarine eutrophication: The balance between enhanced food supply and habitat alterations. *J. Shellfish Res.*, 31(1): 1-11.

Cheng, J. Y. and Demont, M. E. 1996. Hydrodynamics of scallop locomotion: Unsteady fluid forces on clapping shells. *J. Fluid Mech.,* 317: 73-90. https://doi.org/10.1017/S0022112096000663.

Chen, J., Mai, K., Ma, H., Wang, X., Deng, D., Liu, X., Xu, W., Liufu, Z., Zhang, W., Tan, B. and Ai, Q. 2007. Effects of dissolved oxygen on survival and immune responses of scallop (*Chlamys farreri* Jones et Preston). *Fish Shellfish Immunol.*, 22(3): 272-281. doi: 10.1016/j.fsi.2006.06.003.

Epelbaum, A., Pearce, C. M., Yuan, S., Plamondon, N., and Gurney-Smith, H. 2011. Effects of stocking density and substratum on the survival, growth, burrowing behaviour and shell morphology of juvenile basket cockle, *Clinocardium nuttallii*: Implications for nursery seed production and field outplanting. *Aquac. Res.*, 42(7): 975-986. https://doi.org/10.1111/j.1365-2109.2010.02680.x.

Feldesman, M. R. 2002. Classification trees as an alternative to linear discriminant analysis. *Am. J. Phys. Anthropol.*, 119(3): 257-275. https://doi.org/10.1002/ajpa.10102.

Guo, H., Zhang, D., Jiang, S., Li, Y., Zhang, N., Wang, Y. and Ma, Z. 2017. Morphological variations of the winged pearl oyster *Pteria penguin* (Roding, 1798) from South China Sea. *Indian J. Fish.,* 64(1): 9-17. https://doi.org/10.21077/ijf.2017.64.1.51451-02.

Hiebenthal, C., Philipp, E. E. R., Eisenhauer, A. and Wahl, M. 2012. Interactive effects of temperature and salinity on shell formation and general condition in Baltic Sea *Mytilus edulis* and *Arctica islandica*. *Aquat. Biol.,* 14(3): 289-298. https://doi.org/10.3354/ab00405.

Kail, J., Brabec, K., Poppe, M. and Januschke, K. 2015. The effect of river restoration on fish, macroinvertebrates and aquatic macrophytes: A meta-analysis. *Ecol. Indic.*, 58: 311-321. https://doi.org/10.1016/j.ecolind.2015.06.011.

Kakehi, S., Kamiyama, T., Kaga, Y., Naiki, K. and Kaga, S. 2017. Improvement in the dissolved oxygen concentration and water exchange in Ofunato Bay, Japan, after the collapse of the baymouth breakwater by the 2011 Tohoku earthquake and tsunami. *Fish. Oceanogr.*, 26(2): 114-127. https://doi.org/10.1111/fog.12184.

Kock, K. D. and Wolmarans, C. 2007. Distribution and habitats of *Corbicula fluminalis africana* (Mollusca: Bivalvia) in South Africa. *Water SA*, 33(5): 709-715.

Kuznetsova A, Brockhoff, P. B. and Christensen R. H. B. 2015. *lmerTest: Tests in Linear Mixed Effects Models.* https://cran.r-project.org/web/packages/lmerTest/index.html.

Lagos, N. A., Benítez, S., Grenier, C., Rodriguez-Navarro, A. B., García-Herrera, C., Abarca-Ortega, A., Vivanco, J. F., Benjumeda, I., Vargas, C. A., Duarte, C. and Lardies, M. A. 2021. Plasticity in organic composition maintains biomechanical performance in shells of juvenile scallops exposed to altered temperature and pH conditions. *Sci. Rep.*, 11: 24201.

Laing, I. 2002. Effect of salinity on growth and survival of king scallop spat (*Pecten maximus*). *Aquaculture*, 205(1): 171-181. https://doi.org/10.1016/S0044-8486(01)00663-9.

Lessard, J. and Campbell, A. 2007. Describing northern abalone, *Haliotis kamtschatkana*, habitat: Focusing rebuilding efforts in British Columbia, Canada. *J. Shellfish Res.*, 26(3): 677-686. DOI:10.2983/0730-8000(2007)26[677:DNAHKH]2.0.CO;2.

Li, X. L., Shi, H. M., Xia, H. Y., Zhou, Y. P. and Qiu, Y. W. 2014. Seasonal hypoxia and its potential forming mechanisms in the Mirs Bay, the northern South China Sea. *Cont. Shelf Res.*, 80: 1-7.

Liu, S., Lou, S., Kuang, C., Huang, W., Chen, W., Zhang, J. and Zhong, G. 2011. Water quality assessment by pollution-index method in the coastal waters of Hebei Province in Western Bohai Sea, China. *Mar. Pollut. Bull.*, 62(10): 2220-2229.

Lomovasky, B. J., Lasta, M., Valiñas, M., Bruschetti, M., Ribeiro, P., Campodónico, S. and Iribarne, O. 2008. Differences in shell morphology and internal growth pattern of the Patagonian scallop *Zygochlamys patagonica*, in the four main beds across their SW Atlantic distribution range. *Fish. Res.*, 89(3): 266-275.

Lord, J. and Whitlatch, R. 2014. Latitudinal patterns of shell thickness and metabolism in the eastern oyster C*crassostrea virginica*, along the east coast of North America. *Mar. Biol.*, 161(7): 1487-1497.

Lu, Y., Zheng, H., Zhang, H., Yang, J. and Wang, Q. 2016. Cloning and differential expression of a novel toll-like receptor gene in noble scallop *Chlamys nobilis* with different total carotenoid content. *Fish Shellfish Immunol.*, 56: 229-238. https://doi.org/10.1016/j.fsi.2016.07.007.

Lu, W., Li, W., Ke, C. and Wang, H. 2017. Reproductive success under the joint influences of temperature and salinity in noble scallop, *Chlamys nobilis* (Reeve). *Aquac. Res.,* 48(2): 686-696. https://doi.org/10.1111/are.12915.

Luo, X., Ke, C. and You, W. 2013. Estimates of correlations for shell morphological traits on body weight of interspecific hybrid abalone (*Haliotis discus hannai* and *Haliotis gigantea*). *J. Shellfish Res.*, 32(1): 115-118. DOI:10.2983/035.032.0117.

Marie-Orleach, L., Vogt-Burri, N., Mouginot, P., Schlatter, A., Vizoso, D. B., Bailey, N. W. and Scharer, L. 2017. Indirect genetic effects and sexual conflicts: Partner genotype influences multiple morphological and behavioral reproductive traits in a flatworm. *Evolution*, 71(5): 1232-1245. https://doi.org/10.1111/evo.13218.

Marquez, F., Amoroso, R., Sainz, M. F. G., and Molen, S. V. D. 2010. Shell morphology changes in the scallop *Aequipecten tehuelchus* during its life span: A geometric morphometric approach. *Aquat. Biol.*, 11(2): 149-155.

Oldham, T., Oppedal, F. and Dempster, T. 2018. Cage size affects dissolved oxygen distribution in salmon aquaculture. *Aquac. Env. Interac.*. 10: 149-156. DOI: https://doi.org/10.3354/aei00263.

Owada, M., Kasai, Y., Sato, S. and Hong, J. S. 2013. Shell morphology and genetic characteristics of *Corbula* (*Potamocorbula* spp. (Bivalvia: Corbulidae) from the waters adjacent to Japan, Korea and San Francisco Bay. *Aquat. Biol.*, 19(3): 297-305.

Pan, K. and Wang, W. X. 2008. The subcellular fate of cadmium and zinc in the scallop *Chlamys nobilis* during waterborne and dietary metal exposure. *Aquat. Toxicol.*, 90(4): 253-260. doi: 10.1016/j.aquatox.2008.09.010.

Peyer, S. M., Hermanson, J. C. and Lee, C. E. 2010. Developmental plasticity of shell morphology of Selin quagga mussels from shallow and deep-water habitats of the great lakes. *J. Exp. Biol.*, 213(15): 2602-2609. doi:10.1242/jeb.042549.

Peyer, S. M., Hermanson, J. C. and Lee, C. E. 2011. Effects of shell morphology on mechanics of zebra and quagga mussel locomotion. *J. Exp. Biol.*, 214(13): 2226-2236. https://doi.org/10.1242/jeb.053348.

RCore Team 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna: Austria. http://www.R-project.org/.

Selin, N. I. 2013. Features of the shell morphology of *Mytilus trossulus* (Bivalvia: Mytilidae) in the fouling of the alga *Sargassum pallidum*, (Phaeophyceae: sargassaceae). *Russ. J. Mar. Biol.*, 39(1): 45-50. DOI:10.1134/S1063074013010094.

Si, T. V., Pernetta, J. C. and Paterson, C. J. 2013. Status and trends in coastal habitats of the South China Sea. *Ocean Coast. Manage.*, 85(85): 153-163. DOI:10.1016/j.ocecoaman.2013.02.018.

Sigwart, J. D. 2009. Morphological cladistic analysis as a model for character evaluation in primitive living chitons (*Polyplacophora, lepidopleurina*). *Am. Malacol. Bull.*, 27(1-2): 95-104.

SBQTS 2007. *GB17378.4-2007, The specification for marine monitoring, Part 4: Seawater analysis*. State Bureau of Quality Technical Supervision, Standards Press, Beijing: China.

Tan, K., Fu, W., Zhang, H., Ma, H., Li, S. and Zheng, H. 2022. Intraspecific hybridization as a mitigation strategy of low salinity in marine bivalve noble scallop *Chlamys nobilis*. *Aquaculture*, 552: 738037.

Telesca, L., Michalek, K., Sanders, T., Peck S. L., Thyrring, J. and Harper, E. 2018. Blue mussel shell shape plasticity and natural environments: A quantitative approach. *Sci. Rep.*, 8: 2865.

Therneau, T., Atkinson, B. and Ripley, B. 2013. *Rpart: Recursive Partitioning. R Package Version 4.1-3.* http://CRAN.R-project.org/package=rpart.

Tomiyama, T. 2021. Ecophenotypic plasticity in shell growth direction of asari clam *Ruditapes Philippinarum*. *J. Mar. Biol. Assoc. UK*, 101(3): 555-560.

Tremblay, I. and Guderley, H. E. 2017. Possible prediction of scallop swimming styles from shell and adductor muscle morphology. *J. Shellfish Res.*, 36(1): 17-30.

Tremblay, I., Guderley, H. E. and Himmelman, J. H. 2012. Swimming away or clamming up: The use of phasic and tonic adductor muscles during escape responses varies with shell morphology in scallops. *J. Exp. Biol.*, 215(23): 4131-4143. https://doi.org/10.1242/jeb.075986.

Wall, C. C., Gobler, C. J., Peterson, B. J. and Ward, J. E. 2013. Contrasting growth patterns of suspension-feeding molluscs (*Mercenaria mercenaria*, *Crassostrea virginica*, *Argopecten irradians*, and *Crepidula fornicata*) across a eutrophication gradient in the Peconic Estuary, NY, USA. *Estuar. Coast.*, 36: 1274-1291.

Wang, H., Guo, X., Zhang, G. and Zhang, F. 2004. Classification of jinjiang oysters *Crassostrea rivularis* (Gould, 1861) from China, based on morphology and phylogenetic analysis. *Aquaculture*, 242(1): 137-155. DOI:10.1016/j.aquaculture.2004.09.014.

Wang, Y., Fu, D. and Xia, J. 2013. The genetic diversity of the noble scallop (*Chlamys nobilis*, Reeve 1852) in China assessed using five microsatellite markers. *Mar. Genom.*, 9(1): 63-67. doi: 10.1016/j.margen.2012.06.003.

Yu, Z. H., Yang, H. S., Liu, B. Z., Xu, Q. A., Xing, K. and Zhang, L. B. 2010. Growth, survival and immune activity of scallops, *Chlamys farreri* Jones et Preston, compared between suspended and bottom culture in Haizhou Bay, China. *Aquac. Res.*, 41(6): 814-827. doi:10.1111/j.1365-2109.2009.02358.x.

Yuan, T., He, M. and Huang, L. 2009. Intraspecific genetic variation in mitochondrial 16s RNA and COI genes in domestic and wild populations of Huaguizhikong scallop *Chlamys nobilis*, Reeve. *Aquaculture*, 289(1-2): 19-25. DOI:10.1016/j.aquaculture.2009.01.004.

Zhao, L., He, Y., Yang, F., Nie, H. and Yan X. 2014. Correlation and path analysis of morphological and weight traits in marine gastropod *Glossaulax reiniana*. *Chin. J. Oceanol. Limn.*, 32(4): 821-827. DOI:10.1007/s00343-014-3290-4.

Zheng, H., Zhang, T., Sun, Z., Liu, W. and Liu, H. 2013. Inheritance of shell colours in the noble scallop *Chlamys nobilis* (Bivalve: Pectinidae). *Aquac. Res.*, 44(8): 1229-1235.

Date of Receipt : 15.10.2018
Date of Acceptance : 16.02.2023