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RELATIVE GROWTH OF SHELL AND MUSCLE AND POSITIONAL CHANGES OF MUSCLE SCARS DURING SHELL GROWTH OF GREEN MUSSEL, *PERNA VIRIDIS* L.

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Abstract

*Relative growth of shell and muscle of the green mussel (*Perna viridis *L.), along with muscle scar displacement during growth, have been studied in detail. Parameters of 70 small and large mussel valves (2-10 cm) were measured and compared to obtain the following conclusions:*

1. The relative growth rate is faster in the antero-posterior direction than in the dorsoventral and lateral direction of a single mussel shell.

2. Length/depth (L/T) and length/width (L/W) ratios of mussel shell gradually increase with increase in shell length.

3. Maximum depth point (Tmax) of the shell displaces laterally relatively fast in smaller mussel shells (2-4 cm) and displaces laterally relatively slowly in larger mussel shells (4.5-10 cm) at a constant angle of 30 degrees with respect to shell margin plane (Y-axis).

4. There are exponential increases in mussel shell margin plane area, single shell weight and single shell volume with respect to increase in shell length.

5. The specific gravity of smaller mussel shell (2-3 cm) is lower than that of larger shell (4.5-10 cm).

6. There is a specific direction and magnitude of displacement for each muscle scar on the mussel shell. The posterior adductor (p) displaces posteriorly relatively faster than dorsally in all mussel shells studied. The dorsal retractor (d) displaces dorsally relatively faster than posteriorly in the smaller mussel (2-3 cm) and displaces posteriorly relatively faster than dorsally in the larger mussel (3.5-10 cm). The anterior retractor (a) displaces dorsally relatively faster than posteriorly in all the mussel shells studied.

7. The p displaces away from the umbo (u) at a relatively faster rate than the d and the d displaces away from the umbo at a relatively faster rate than the a.

8. The distance from the umbo to each muscle scar and the pallial line tip and the distances between the muscle scars increases linearly proportional to the increase in mussel shell length.

9. Cross-sectional area of each muscle bundle (a, d, p), as indicated by the area of the muscle scars increases exponentially with respect to shell length and increases linearly with respect to the shell margin plane area. The area of p increases relatively faster than that of d, and that of d increases relatively faster than that of a.

Data are discussed based on theories of biological pattern formation and positional information proposed by several investigators.

Introduction

The green mussel, *Perna viridis* L.[1] used in this study is a food eaten by Southeast Asian peoples. It is abundant along the seashore of Chon Buri, Samut Prakarn, Samut Sakorn, and Samut Songkram where many rivers empty into the Gulf of Thailand. The shell of this species of mussel is bright green at the shell margin and brown near the umbo and there are conspicuous concentric growth rings. The green mussel has byssus threads for holding substrates in the tidal zone of the seashore. It can grow 8-10 cm in a year. The shell of green mussel is pointed anteriorly and fans out postero-dorsally. The ventral shell margin remains relatively linear during growth.

As in other bivalves[3-9] the shell forms from the mantle. Shell formation begins with an organic matrix produced by mantle deposited as lamella on the shell surface then layers of calcium carbonate are deposited alternating with layers of organic matrix. The calcium carbonate is first laid down as small crystals which then grow and unite to form a crystalline layer that eventually becomes the columns of the middle prismatic layer. The column is laid down at right angles to the inner laminated layer. The calcium carbonate may occur as calcites, aragonite or vaterite, the crystalline form is determined by the chemical nature of the shell organic matrix. The forward edge of the mantle, which secretes both organic and inorganic components, forms the growing edge of the shell. The innermost or nacreous layer, which is mostly in the form of aragonite of calcium carbonate, may be laid down as plates forming prisms that reflect light. The nacreous layer is secreted by scattered cells all over the outer lobe of the mantle.

This report is concerned with the relative growth rate of the shell in terms of length (L), width (W), shell margin plane area, shell volume and shell weight. Data on the displacement of the pallial line, which is the attachment of the muscular mantle edge[10], is included. Changes in muscle scar area in relation to shell growth are also analyzed. A similar study has been reported by Maynard and Burke[11] on the giant clam *Tridacna gigas* on muscle weight relative growth rate. The changes in the coordinates of each muscle scar, and the maximum depth point (Tmax) are also presented. The procedure used here may be adapted to analyse morphogenesis, pattern formation and positional information processes in animals and plants according to theories proposed by several investigators[12-22] .

The relationships among parameters of the muscle scars and shells hereby studied could be used as models in similar studies in the muscles and bones of higher animals.

Materials and Methods

About seventy green mussels *Perna viridis* of various sizes (2-10 cm long) were obtained from a market in Bangkok, Thailand. Shells were prepared for study by boiling and then removing viscera. The shells were then sun dried for 2-3 weeks, then cleaned free from dust before studied in the laboratory. Only the right valve of each mussel was used in this study assuming that the data should be the same for the left valve. Numbers (1; 2, 3......) were written with pencil on each shell randomly as identification number for each individual shell. Shells were laid flat on a piece of paper and then the outline was traced. The identification number of the shell was written on the tracing. The length and width were measured (see Fig. 1). The depth (T) was measured by inserting the shell between two parallel flat boards, the shell margin resting on one of these and the other board touching the point on the shell furthest (Tmax). The depth from the margin plane to the Tmax is the distance between the two boards. (See Fig 1, II). $Y\hat{U}T\mathrm{max}$ angle was measured with a transparent protractor. The centre of the protractor was laid on the umbo (U) and the line extending from the centre to 0° was aligned with the projection point of Tmax on the shell margin plane so named the Y-axis. The angle between Tmax point and the Y-axis were read as $Y\hat{U}T\mathrm{max}$ when the plane of the protractor was held perpendicular to the shell margin plane. With the shell held in this position the distances of U-Tmax, U-Tmax at Y and Tmax-Tmax at Y were also measured.

The area of the shell margin plane was found by cutting the tracing paper along the shell margin outline and then weighing this piece of paper and multiplication of this weight by the constant area/weight of the paper gave the shell margin plane area.

The specific gravity of each shell was obtained by dividing shell weight in air by the weight of water displaced by the shell.

The name of each muscle scar, is identified according to Standbury[2] namely the anterior retractor (a), the dorsal retractor (d) and the posterior adductor (p) scars. The outline of each muscle scar was drawn clearly using pencil and the centre of each scar was marked (See Fig. 1, I). A transparent protractor was placed on the shell with its centre on the umbo (U). The line on the protractor extending from the centre to 0° was laid on the ventral margin of the shell, which was taken as the X-axis. Then the angles between muscle scar centres and the X-axis were read (namely $X\hat{U}a$, $X\hat{U}d$ and $X\hat{U}p$). The coordinates of the muscle scars (a, d, p) namely U-ax, a-ax; U-dx, d-dx; U-px, p-px, were read. The distances U-a, U-d, U-p, U-pallial line tip, a-d, a-p, d-p, were also measured.

The areas (A) of muscle scars (Aa, Ad, Ap) were measured by lining a transparent graph paper upon the scar.

Results

The relative growth of the shell of the green mussel *P. viridis* in terms of length (L), width (W) and depth (T) are shown in Fig. 2. The relative Growth in the antero-posterior direction (length) is greater than in the dorso-ventral direction (width) and the relative growth in the dorso-ventral direction is greater than that in the lateral direction (depth). Fig. 3 shows that L/W and L/T ratios increase gradually with increase in shell length. This indicates that there is acceleration of shell growth in the antero-posterior direction.

Changes in the coordinates of the maximum depth point (Tmax) (the U-Tmax at Y, Tmax to Tmax at Y) are shown in Fig. 4. In smaller mussels (2-4 cm shell length), the Tmax coordinate displaces laterally relatively fast, but in larger mussels (4-10 cm in length) the lateral displacement is relatively slower. Observation of the concentric growth rings (See Fig. 1) indicates that the increase in shell depth may be due to accumulation of shell material medially (near the shell margin plane). This may cause the Tmax to move postero-laterally as seen in Fig. 4.

The Y$\hat{U}$Tmax is large in small mussel shells (2-4 cm) (Fig. 5) then the Y$\hat{U}$Tmax reduces to a relatively constant 30 degree angle in the larger shells (4.5-10 cm long). Fig. 6 shows that the decrease in Y$\hat{U}$Tmax in mussel shells 2-4 cm in length is due to a relatively fast increase in the U-Tmax at Y distance while the Tmax-Tmax at Y distance increases relatively slowly. Afterwards, the U-Tmax at Y and Tmax to Tmax at Y increases at about the same relative rate, this may give constant Y$\hat{U}$ Tmax angle in shells 4-10 cm in length. Fig. 6 also shows that the increase in U-Tmax is parallel to an increase in U-Tmax at Y.

The relationship between shell length and the shell margin plane area is shown in Fig. 7. This figure demonstrates that the shell margin plane area increases exponentially with increase in shell length. The shell weight and volume (Figs. 8 and 9, respectively) also increase exponentially with respect to increase in shell length. The shell margin plane area, the weight and the volume increase relatively slowly in small mussels (2-5.5 cm) then relatively quickly in larger mussels (5.5-10 cm). The specific gravity of the shell (Fig. 10) is less in very small shells (2-3 cm) and becomes relatively constant between 2.0-2.5 in larger shells (3.5-10 cm).

Fig. 11 shows changes in the coordinates of three muscle scars, namely, the anterior retractor (a), the dorsal retractor (d) and the posterior adductor (p) where the ventral shell margin is set as the X-axis and the umbo (U) as the origin (0, 0) (See Fig. 1). This figure simulates positional changes of each muscle scar on the shell during growth. The direction of displacement of each muscle scar is indicated by a least square fit line in Fig. 11. It can be seen that "a" displaces dorsally more than posteriorly, whereas

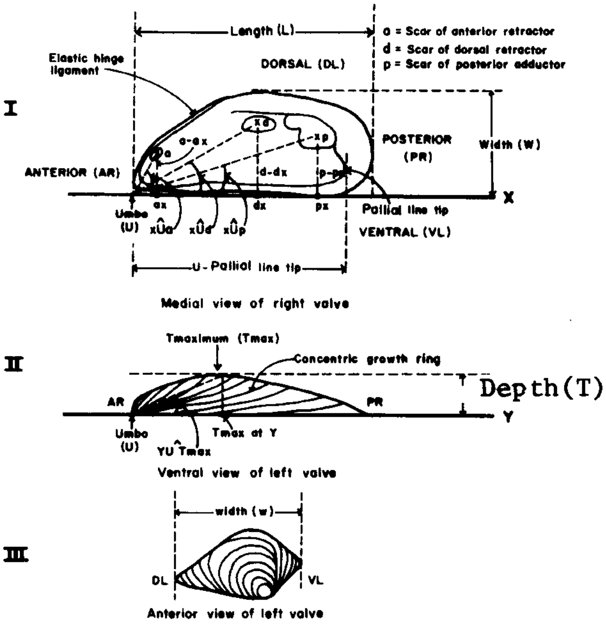

Fig 1. The illustration of various shell and muscle parameters investigated in the green mussel. Perna viridis L. Locations of shell length (L), width (W) and depth (T) measurements are indicated.

The middle (II) figure shows the location of maximum depth point (Tmax). The Y-axis is on the shell margin plane and passing the projection point of Tmax on the shell margin plane and the umbo (U). YU Tmax angle and Tmax at Y which is projection point of the Tmax on the Y-axis are shown.

The lower (III) figure shows the anterior view of the left mussel valve and its cocentric growth rings.

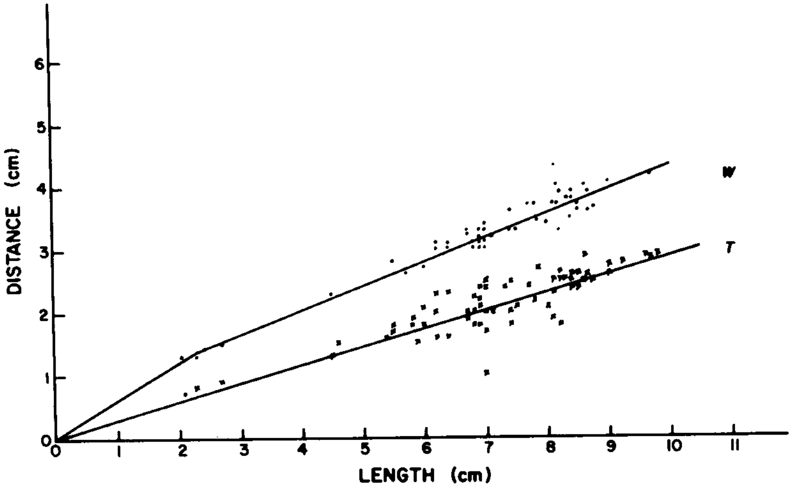

Fig 2. Relationships of the green mussel shell length (L), width (W) and depth (T). The increase in the length (L) is relatively greater than in the width (W) and increase in the width (W) is relatively greater than in the depth (T).

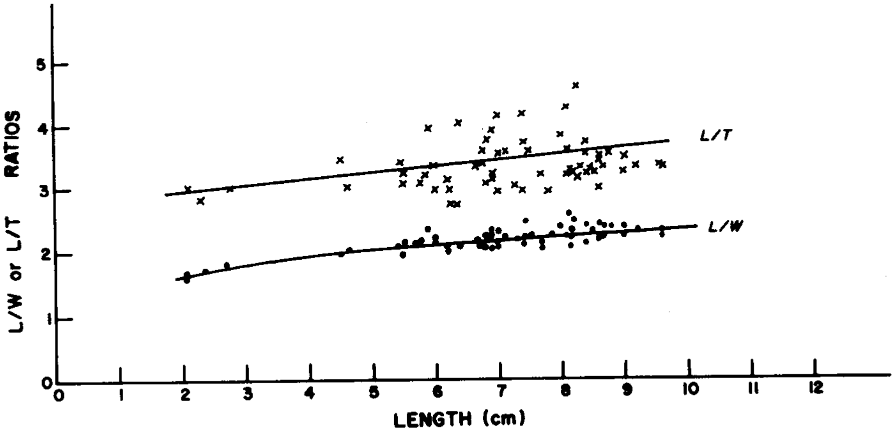

Fig 3. The relationship of the mussel shell length (L) and the length/width and length/depth ratios. These ratios increase gradually with increase in the shell length.

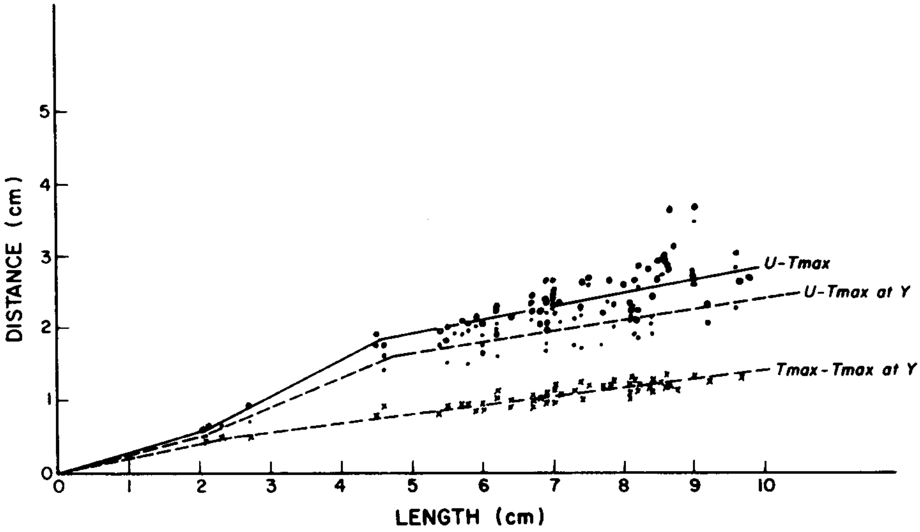

Fig 6. Changes in the U-Tmax, the U-Tmax at Y, and the Tmax-Tmax at Y The same data as in Fig 4, and the U-Tmax are plotted as function of the mussel shell length.

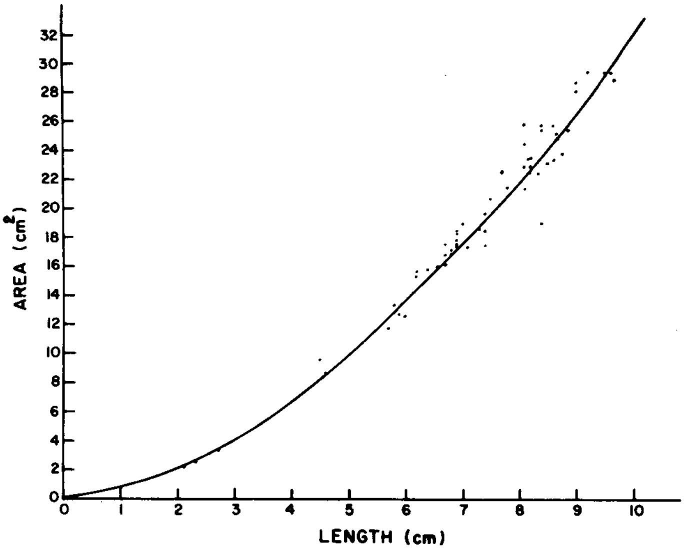

Fig 7. The relationship between mussel shell length (L) and the shell margin plane area. Exponential relationship is shown.

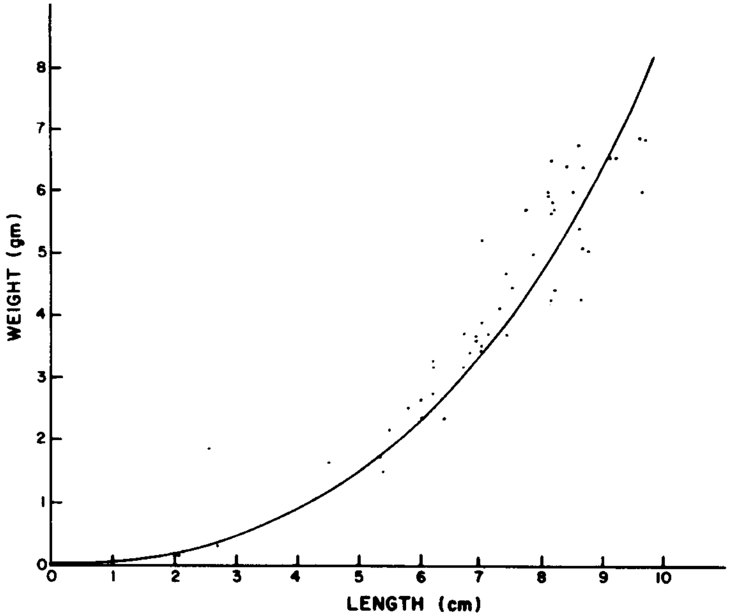

Fig 8. The relationship between the mussel shell length (L) and the single shell weight. There is exponential relationship between the shell length and the shell weight.

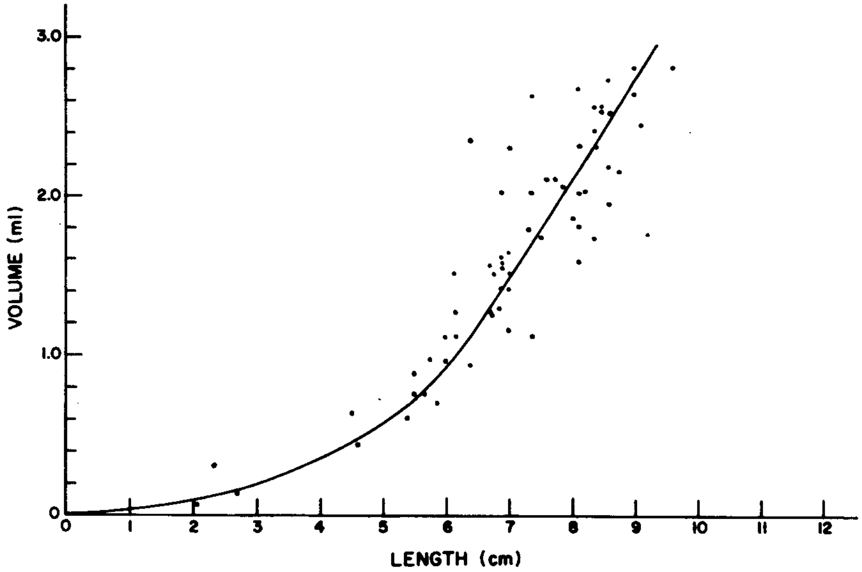

Fig 9. The relationship between the mussel shell length and the single shell volume. There is exponential relationship between the shell length and its single valve volume.

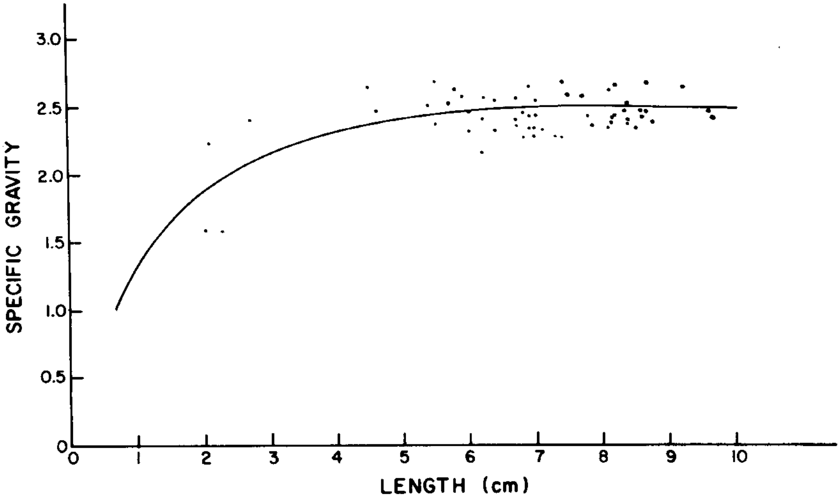

Fig 10. The specific gravity of the mussel shell at different shell length. The specific gravity of shells larger than 4 cm. is relatively constant at 2.4. The specific gravity of shells smaller than 3 cm. is less.

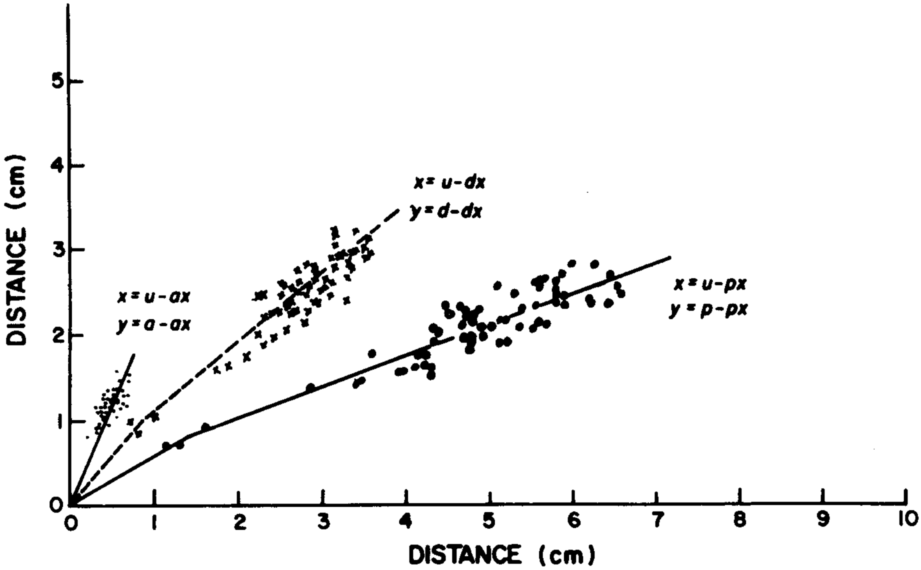

Fig 11. Coordinates of the mussel anterior retractor muscle scar (a) (left), the dorsal retractor muscle scar (d) (middle) and the posterior adductor scar (p) (right). There are specific directions and magnitude of positional changes during growth of the a, d and p. The ventral shell margin was set as the X-axis and the umbo (U) as 0, 0 origin point.

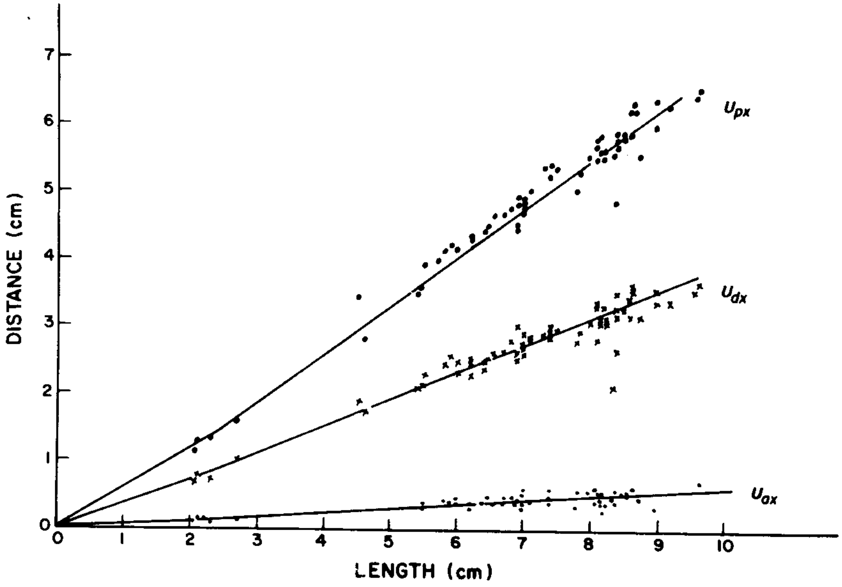

Fig 12. Relationships between the mussel shell length and distances from the umbo (U) to projections of a, d, and p on the X-axis (sx, dx, px). There are linear relationships between the shell length and the Uax, Udx and Upx.

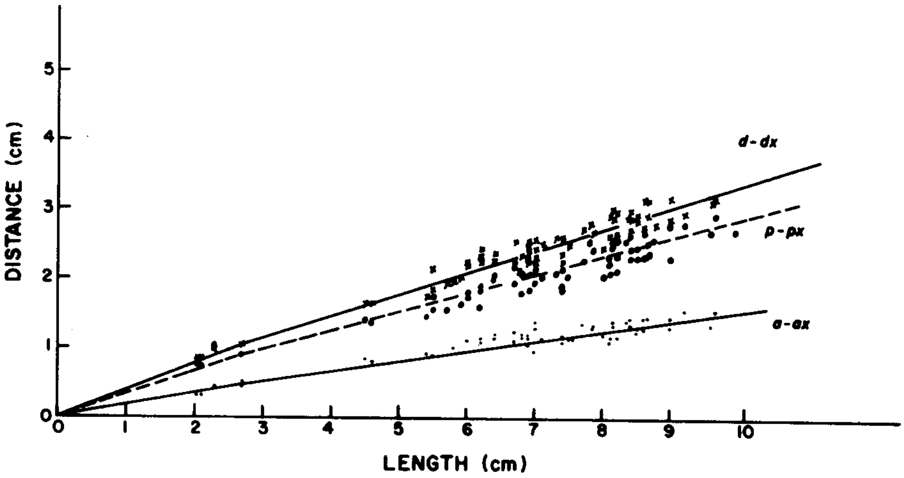

Fig 13. Relationships between the mussel shell length and distances from a, d, p muscle scars to X-axis. There are approximately linear relationships of a-ax, d-dx and p-px with the shell length.

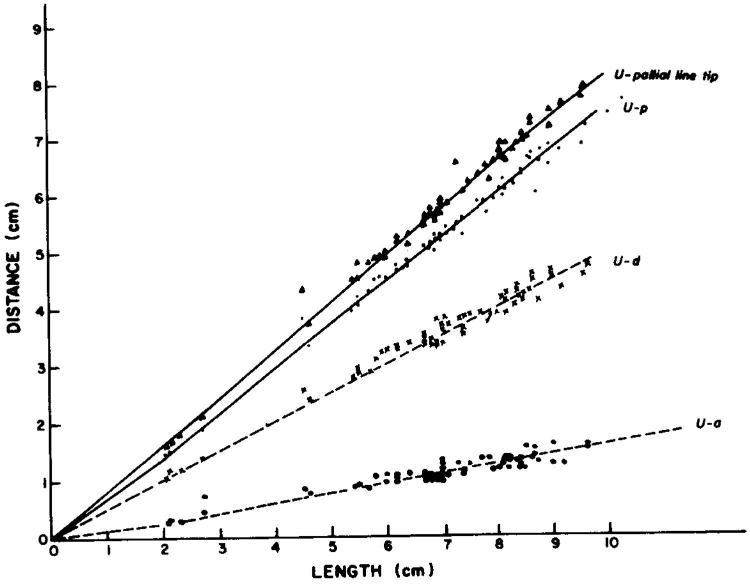

Fig 14. Relationships between the mussel shell length and distances from the umbo (U) to a, d, p and pallial line tip. There are approximately linear correlation between the shell length and the U-a, U-d, u-p and u-pallial line tip.

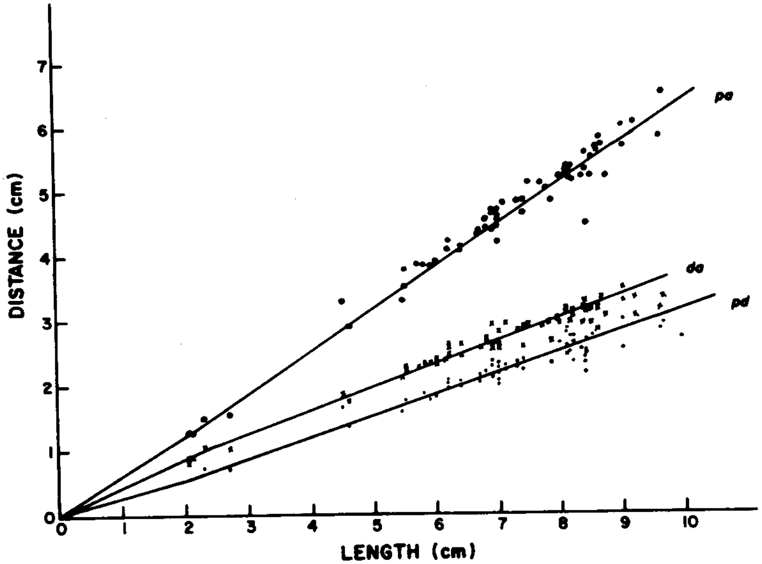

Fig 15. Relationships between the mussel shell length and distances among muscle scars. There are approximately linear correlation between the shell length and pd, da and pa.

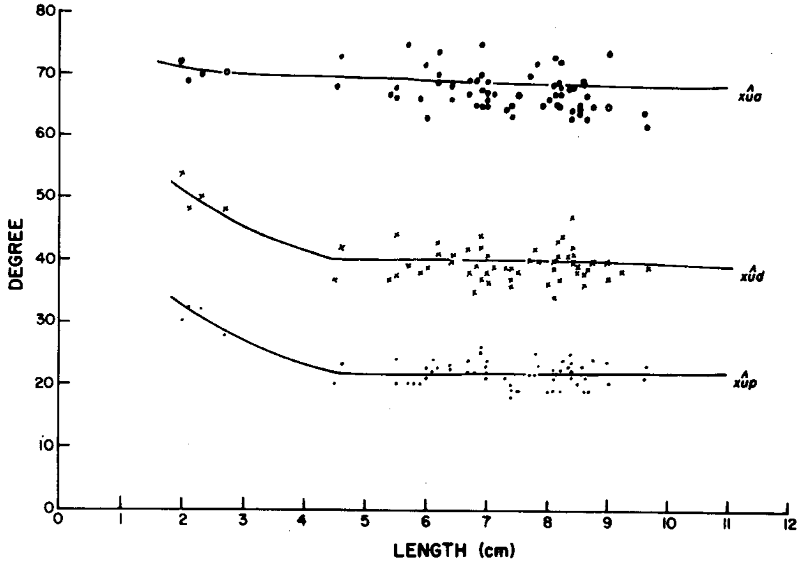

Fig 16. Relationships between the mussel shell length and each muscle scar to umbo and X-axis angles. There are two obvious phases of angle changes during growth for the d and p but not so obvious for the a.

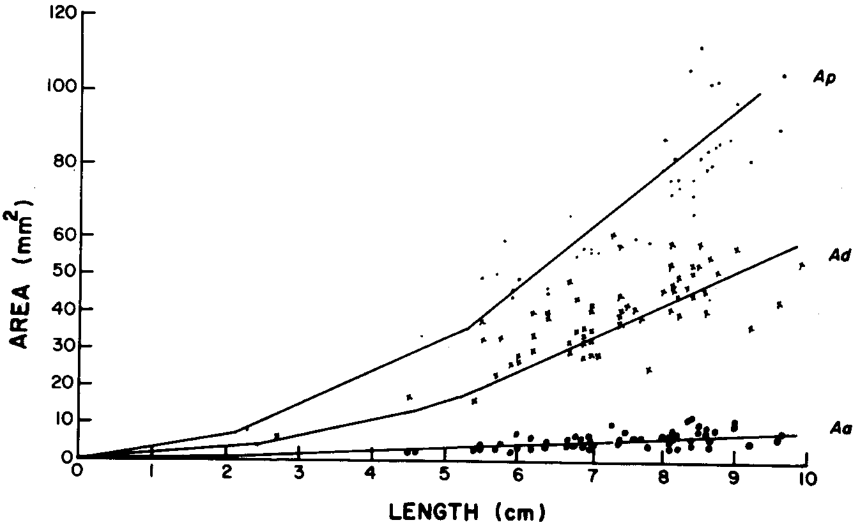

Fig 17. Relationships between the mussel shell length and areas (A) of a, d, p. muscle scars. There are exponential increments in the Aa, Ad, and Ap with respect to the shell length.

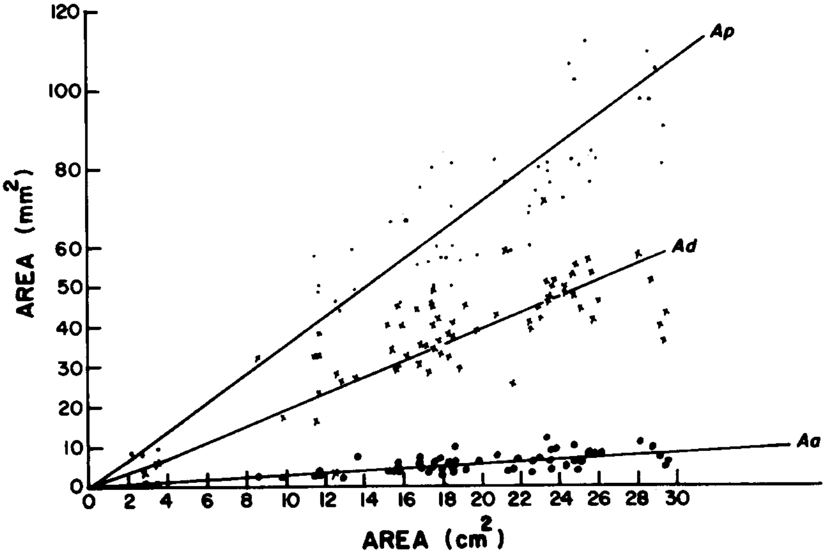

Fig 18. Relationships between the mussel shell margin plane area and muscle scar areas. There are linear correlations between the shell margin plane area and muscle acar areas (Aa, Ad and Ap).

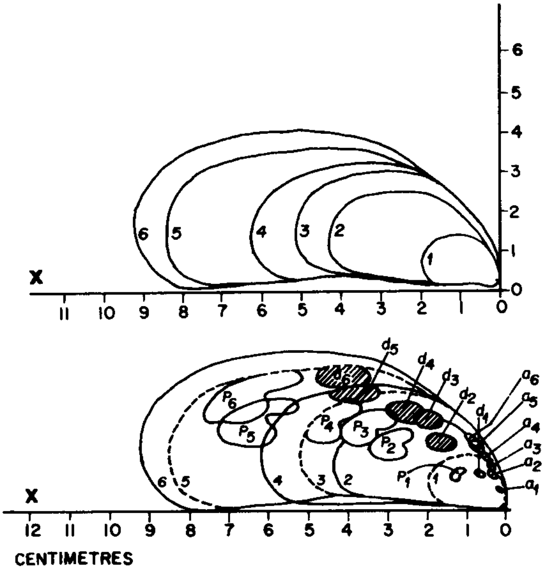

Fig 19. The summary of the right mussel shell Composite outlines of various shell size and muscle scar outlines along with the positions of muscle scars. Most data presented in previous figures can be visualize from this figure.

"d" displaces dorsally more than posteriorly in smaller mussels and posteriorly more than dorsally in larger mussels. The "p" displaces relatively faster posteriorly than dorsally in all sizes of mussel studied. Thus, though any individual shell has but one scar for each of the muscles, the composite in Fig. 11 clearly shows muscle scars move during growth. This may indicate effective repair of old muscle scars after displacement of the muscle attachment has occured, therefore, at each period of growth there is only one muscle scar seen for each muscle at that point of time. Further analyses of muscle scar displacement during growth are shown in Figs. 12 and 13. Fig. 12 analyzes displacement of each muscle scar posteriorly and Fig. 13 dorsally. Conclusion similar to that of Fig. 11 can be drawn from Figs. 12 and 13.

Fig. 14 shows the distances of displacement of a, d, p, and pallial line tip from the umbo (U) (U-a, U-d, U-p, U-pallial line tip). The increase in the distances between the umbo and each muscle scar and the pallial line tip is proportional to the increase in mussel shell length. In each case the relationship is approximately linear. The distance between each pair of muscle scars (pa, da and pd) (Fig. 15) is also proportional to the shell length and again the relationship is approximately linear.

Fig. 16 shows changes in the $X\hat{U}a$, $X\hat{U}d$ and $X\hat{U}p$ with respect to shell length. It can be seen that $X\hat{U}a$ is relatively constant during growth whereas $X\hat{U}d$ and $X\hat{U}p$ of smaller mussel shells (2-4.5 cm.) decrease gradually then become relatively constant afterwards in larger mussels (also see Fig. 1, 11 and 19).

Muscle scar area which is presumably the muscle bundle cross-sectional area of a, d and p increases exponentially with respect to shell length (Fig. 17) and linearly with respect to shell margin plane area (Fig. 18). The increase in the muscle scar area is greater in p than in d and in d than in a.

Fig. 19 summarizes most of the data presented in the previous figures concerning shell and muscle growth along with muscle scar positional changes during growth.

Discussion

Increase in the green mussel shell length (L) is relatively faster than increase in width (W) and depth (T). This may be caused by the shape and distribution of mantle, from which the shell is formed[2]. It may be partly explainable by a theory proposed by Summerbell[12] stating that genome controls functions of the cell; products made by the cell create an environment that in turn modifies the functions of the genome and the cell itself. The shell made by the mantle acts as barrier to lateral growth of mussel viscera and the curved anterior, dorsal and ventral margins of the shell act as barriers to visceral growth in these directions and visceral growth is least opposed in the posterior direction. Consequently the mantle tends to distribute posteriorly and since the mantle is the shell-producting organ, shell growth is relatively faster in this direction. There seems to be acceleration of the relative growth in the antero-posterior direction as can be seen from the gradually increasing L/W and L/T ratios with respect to shell length

(Fig. 3). This may indicate an increase in the shell forming capacity of the mantle of the larger mussel. It has been shown in the pond snail *Lymnaea stagnalis* that growth of shell is under control of a growth hormone[23]. There is still no report whether or not the growth of the mussel is controlled by growth hormone. If it is also true for the mussel as in the case of the pond snail, it is possible that the growth hormone level may be enhanced in the larger mussels.

Changes in Tmax coordinate indicate that there are two major phases of depth growth. The growth in the lateral direction is relatively faster in mussels 2-4 cm long and relatively slower in mussels larger than 4 cm. Increase in mussel shell depth may be due to the accumulation of newly made shell upon old shell margin medially as is evident from the concentric growth ring orientation. The two phases of Tmax positional change may be due to combinations of two major factors, firstly, differences in the relative rates of new shell formation medial to the old shell margin and, secondly, differences in the geometry of newly-formed versus previously-formed shell. Evidence of these latter may be observed in the differences in the shape of the shell at the umbo and at the posterior margin of the larger shell.

The greater relative rate of increase in U-Tmax at Y than the Tmax-Tmax at Y may be due to the greater relative rate of antero-posterior growth of the shell.

The exponential increase in shell margin plane area, weight and volume in relation to shell length may reflect an exponential increase in biosynthetic capacity of the mussel during growth. In otherwords, the larger mussels may be able to synthesize shell material relatively faster than are smaller ones.

The difference in the specific gravity of the shells of smaller mussels and larger ones may be due to differences in shell composition compactness. In the future, detail chemical analyses of the large and small shells may explain the difference observed.

The magnitude and direction of muscle scars displacement during growth are predictable. The differences observed may be caused by many factors, such as barriers created by the shell geometry and pressure put on each muscle bundle by visceral growth. The anterior retractor (a) displacement is limited by the curve of the shell dorsally and ventrally near the umbo. Change in positions of the dorsal retractor (d) and posterior adductor (p) may no be so constrained by the shell shape. There may also be facilitation of muscle bundle displacement by pressure exerted by growing visceras on a, d, and p in the directions observed.

The fact that old muscle scars are not seen in a shell indicates effective shell repair after the muscle attachments have moved to new positions.

It can be predicted that each part of a given muscle bundle may have different relative growth rates in different directions. The maximum relative growth rate may be in the direction observed in Fig. 11, whereas the side of the muscle bundle opposite to the direction may degenerate. This prediction could be proved by ultrastructural study of each muscle bundle in the future.

Detailed analyses of factors determining magnitude and direction of each muscle attachment's displacement on the shell during growth have to be analyzed extensively before correct explanations could be offered.

There are linear relationships between shell length and distance from the umbo (U) to a, d and p. as well as distances between each pair of muscle scars. This could indicate that the spreading of muscle attachments is limited by available space on the shell. It also could indicate that there are factors generated by each of the muscle bundle which regulate the spacing.

The decrease in $X\hat{U}d$ and $X\hat{U}p$ in smaller shells (2–4 cm) may be due to an abrupt change in shell geometry during growth. Changes in the geometry of larger (4–10 cm) shells may be such that the muscle attachment displacement angle remains constant relative to the umbo (U) and ventral shell margin (X-axis).

The relative growth rates of a, d and p muscle scars as indicated by changes in their areas with respect to the shell length are different from each other. The relative rate is greater in p than in d and in d than in a. Increase in Aa, Ad and Ap are proportional linearly to the shell margin plane area and exponentially to shell length. Data which are similar to hereby reported are not yet located, however, relative growth of muscle weight in relation to shell weight of the giant clam *Tridacna gigas*[11] has been reported. The data obtained indicate that size of each muscle bundle is determined at least partly by the space available on the shell. The exponential increase in muscle scar area relative to shell length may reflect an exponential increase in muscle bundle volume and weight.

The last figure summarizes most data presented graphically above. Shell and muscle scar growth along with muscle scar positional changes are shown. The top figure in Fig. 19 was obtained by superimposing the outlines of several individual right shells. This is very similar to the concentric growth rings of a large mussel shell (Fig. 1). This indicates medial accumulation of new shell synthesized by the mantle upon the old shell.

The ways these parameters of the shell and of the muscle attachments change during growth could be explained at least partly by theories concerning morphogenesis, pattern formation, and positional information proposed by Summerbell in 1981[12], Honda in 1973[14], Meinhardt in 1978[13], Raff in 1977[15], Cooke and Zeeman in 1976[16], Martynov in 1975[20] and Wilby and Ede in 1975[17]. Detailed analyses of relationships among muscle scars and shells in this study could be used as models for studies on relationships among muscles and bones in higher animals. Similar studies in other species of invertebrates and vertebrates may give greater understanding on interactions among muscles and exo-or endo- skeletons attached by those muscles.

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บทคัดย่อ

ได้ศึกษาการเจริญเติบโตสัมพัทธ์ของเปลือกและรอยกล้ามเนื้อของหอยแมลงภู่ *(Perna viridis* L.*)* พร้อมกันนั้นได้ศึกษาการเปลี่ยนตำแหน่งของรอยกล้ามเนื้อบนเปลือกหอยอย่างละเอียด

ได้ทำการวัดพารามีเตอร์หลายอย่างจากเปลือกซีกขวาของหอยแมลงภู่ ขนาดต่าง ๆ (2-10 ซม.) ประมาณ 70 ตัวได้เปรียบเทียบข้อมูลระหว่างหอยขนาดต่าง ๆ เพื่อให้ได้ข้อมูลของการเปลี่ยนแปลงระหว่างการเจริญเติบโต ผลพอสรุปได้ดังนี้

1. มีอัตราการเติบโตสัมพัทธ์ตามความยาวของหอยมากกว่าความกว้างและความหนาของฝาหอยซีกเดียว

2. อัตราส่วนความยาว/ความกว้างและความยาว/ความหนา ของเปลือกหอยแมลงภู่สัมพัทธ์กับความยาวมีค่าเพิ่มขึ้นเรื่อย ๆ เมื่อหอยโตขึ้น

3. จุดที่มีความหนาสูงสุดเคลื่อนไปในทิศทางด้านข้างสัมพัทธ์กับความยาวในหอยตัวเล็ก (2-4.5 ซม.) จุดนี้เคลื่อนไปทางด้านข้างสัมพัทธ์กับความยาวช้าลงเมื่อหอยโตมากขึ้น (4.5-10 ซม.) โดยทำมุมคงที่ประมาณ 30 องศาจากพื้นราบของขอบฝาหอย

4. มีการเพิ่มพื้นที่พื้นราบของขอบฝาหอย น้ำหนักฝาหอยและปริมาตรแบบเอ็กโพเนนเซียลเมื่อเทียบกับการเพิ่มความยาวของเปลือกหอย

5. เปลือกหอยแมลงภู่ขนาดเล็ก (2-3 ซม.) มีความถ่วงจำเพาะน้อยกว่าเปลือกหอยใหญ่ (4.5-10 ซม.)

6. ทิศทางและขนาดของการเปลี่ยนตำแหน่งของรอยกล้ามเนื้อแต่ละมัดสัมพัทธ์กับความยาวระหว่างการเจริญเติบโตแตกต่างกันดังนี้

   - Posterior adductor (p) เคลื่อนไปทาง posterior สัมพัทธ์กับความยาวเร็วกว่าไปทาง dorsal ตลอดเวลา, dorsal retractor (d) เคลื่อนไปทาง dorsal สัมพัทธ์กับความยาวเร็วกว่าไปทาง posterior ในขนาด 0-3 ซ.ม. แล้วเคลื่อนไปทาง posterior สัมพัทธ์กับความยาวเร็วกว่าไปทาง dorsal ในหอยขนาด 3.5-10 ซ.ม. ส่วน anterior retractor (a) เคลื่อนที่ไปทาง dorsal สัมพัทธ์กับความยาวเร็วกว่าทาง posterior ตลอดเวลา

7. รอยกล้ามเนื้อ (p) เคลื่อนห่างจาก Umbo (U) สัมพัทธ์กับความยาวเร็วกว่ากล้ามเนื้อ d และกล้ามเนื้อ d เคลื่อนที่ห่างจาก Umbo สัมพัทธ์กับความยาวเร็วกว่ากล้ามเนื้อ a

8. ระยะระหว่าง Umbo ถึง muscle scar และ pallial line tip รวมถึงระยะห่างระหว่างรอยกล้ามเนื้อมัดต่าง ๆ เพิ่มขึ้นเป็นสัดส่วนโดยตรงกับการเพิ่มความยาวของเปลือกหอย

9. พื้นที่ภาคตัดขวางของกล้ามเนื้อแต่ละมัด (a, d, p) ที่หาได้จากการวัดพื้นที่ของรอยกล้ามเนื้อบนเปลือกหอยมีการเพิ่มขนาดแบบเอ็กโพเนนเซียล เมื่อเทียบกับความยาวของเปลือกหอย และเพิ่มขึ้นเป็นสัดส่วนโดยตรงกับพื้นที่ราบของขอบฝาหอย พื้นที่ภาคตัดขวางของกล้ามเนื้อ p เพิ่มขึ้นสัมพัทธ์กับพื้นที่ราบของฝาหอยเร็วกว่าของ d และของ d เพิ่มขึ้นสัมพัทธ์กับพื้นที่ราบของฝาหอยเร็วกว่าของ a

ได้พยายามอธิบายข้อมูลที่ได้โดยอาศัยทฤษฎี biological pattern formation และ positional information ที่เสนอไว้โดยนักวิทยาศาสตร์หลายท่าน