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TEMPORAL VARIATION IN SHELL GROWTH RATE OF COCKLE ANADARA GRANOSA IN RELATION WITH ITS REPRODUCTIVE CYCLE M. REZA MIR ZAEI, 1 * AILEEN TAN SHAU HWAI 2 AN D MUNAWA R KH ALIL 3 1 Iranian Fisheries Research Organization, Offshore Fisheries Research Center, 9971956663 Chabahar, Sistan and Baluchestan, Iran; 2 Marine Sciences Laboratory, School of Biological Sciences, Universiti Sains Malaysia, 11800, Minden, Penang, Malaysia; 3 Department of Aquaculture, Universitas Malikussaleh, Reuleut Aceh Utara, Aceh, 24351, Indonesia ABSTRACT A study was conducted on the

relationship between the reproductive cycle and shell growth rate of Anadara granosa (Linnaeus, 1758). Gonadal maturity stages, increment width, and environmental factors were examined by means of a ?eld enclosure experiment in Balik Pulau, Penang Island, Malaysia, from December 2011 to November 2012.

Histological analysis of gonads showed that gametogenic activity of A. granosa occurred throughout the year, with maximum spawning activity observed from April 2012 to late June 2012 (15%–28%) in males and from March 2012 to late June 2012 (19%–44%) in females. Shell cross-section analysis showed that the increment widths of both sexes in the growing group (indeterminate and developing stages) and the spawning group (ripe and spawning stages) ranged from 35–57 to 8–17 m m, respectively.

Seawater temperature and salinity recorded on a daily basis throughout the study period ranged from 22–33°C and 29–31, respectively. A comparison of increment width and gonad development stages in different environmental conditions showed that shell growth in the growing group decreased when seawater temperature and salinity decreased slightly. In contrast, increment widths in the spawning group were much narrower and were in?uenced by energy consumption during ripe and spawning stages.

This study shows spawning breaks in shell structure are considered markers for identifying the period of sexual maturity. Therefore, spawning breaks are suitable proxies for interpretation of the temporal changes in shell microgrowth lines in terms of reproductive cycle of cockle and understanding the number of spawning periods throughout the year. KEY WORDS: cockle, Andara granosa, reproductive cycle, shell microgrowth increment, growth pattern, spawning season INTRODUCTION Growth of aquatic animals can be observed using the growth lines that appear in the shells of molluscs and in the otolith and scales of ?sh species. Growth lines in animals can give a good indication of their life cycles, as well as environmental factors that in?uence their life histories (Mirzaei et al. 2015).

The high- r es o lut io n va ri ati on s i n r es p ons e t o env ir on m ent a l a nd p h ys i o l o g i c a l ch a n g e s i n c o c k l e s h e l l s ma k e t h e m a go o d representative species for examining how these changes in?u- ence growth (Gibson et al. 2001, Sch €one et al. 2003, Witbaard et al. 2005, Ambrose et al. 2006, Gosselin et al. 2006, Limpanont et al. 2010, Karney et al. 2011, Liu et al. 2011). Cockle shells p ossess a series of lines, termed ‘‘microgro wth lines’’ interspaced by ‘‘growth increments’’ (i.e., the area be tween two m icrogrowth lines), w hich can be clearly vie wed in shell sections (Lavaud e t al. 2013).

M icrogrowth lines are darker and n arrower than the growth increments, which are t hic

ker and a re located between the microgrowth lines. Cockle shells grow according t o th e production of co nsecu tive microgrowth lines and g ro wth in c remen ts, which t ogeth e r c an be considered as a growth pattern. Growthpatterns are typically in?u enced by local en vironmental c onditio ns or physiological ch a ng e s s u c h a s r e- produc t ion (Ka naz awa & S at o 200 8, Mirz ae i & Sha u Hwa i 2 01 5).

Interruptions in growth patterns can appear due to environ- mental changes including thermal shock, excessively hot or cold seasons, neap and spring tides, shell margin abrasions, and spawning period (Gibson et al. 2001). However, the formation of irregular microgrowth lines is less affected by environmental factor s and more closely related to physiological activities, esp ecia ll y r epr odu ct ion (Cer rat o et al . 199 1, Sch €one et al . 2005). Physiological changes during the reproductive season have a negative effect on the pattern of shell growth. Speci?cally, spawning breaks are visible in most cockle shells as microgrowth line production ceases during spawning (Thompson et al.

1980, Sa to 19 95 , S ch€one et al. 2005, Nishida et al. 2012). An analysis of the impact of reproduction on the various aspects of shell growth is important for both studies of life history and morphological evolution. However, very few studies have assessed the relation- s hi p b e tw ee n s he ll m i cr og ro wt h l in es a n d r ep ro du ct i v e c yc le i n marine molluscs [but see studies on Tellin nitidotellina nitidula (Kawai et al. 1993) and Phacosoma japonicum (Sa t o 1 99 5)]. In Pe ni ns ul ar M al ay s i a, A na da ra gr an os a of t he f am il y Arcidae is a commerci ally im portant specie s.

Bloo d coc kle production in 2008 reached the highest value of USD 28 million, whereas it reached to USD 23 million in 2011 (Mirzaei et al. 2015). The reproductive cycle of A. granosa varies geographi- cally (Suwanjarat et al. 2009, Khalil 2013). Thus, analyses of the physiological and environmental impacts on the growth of A. granosa are important for studies of both life history and morphological evolution. Therefore, it is necessary to determine the pattern of maturity and spawning season and their relation- ships with environmental factors. In this study, the different maturity stages of A.

granosa and the impact of local environ- mental changes and spawning breaks on the microgrowth lines in their shell structure were investigated. MATERIALS AND METHODS Site Preparation and Sample Collection A total of 600 similarly sized Anadara granosa (; 10 mm) were stained with shell dye (Alizarin Red) at a concentration of *Corresponding author. E-mail: mirzaei.mr@gmail.com DOI: 10.2983/035.036.0109 Journal of Shell?sh Research, Vol. 36, No. 1, 69–78, 2017. 30 ppm before being transferred to the study site. The cockles were placed in a plastic mesh cage (1.5 m 3 1.5

m 3 2 m) located at an intertidal site (exposed during all low tides) in Balik Pulau (5 °

20#05.50 ## N, 100° 11#35.32## E), Penang Island, Malaysia (Fig. 1). Forty samples were collected each month between December 2011 and November 2012. In the laboratory, soft tissues were gently removed from inside the shells and were used for histological examination and shell valves were prepared for shell cross-sectioning. Histology Histological analysis was carried out according to the pro- tocol described by Matias et al. (2013). The gonadal tissue was cut into small pieces (5 mm) and immediately immersed in Bouin Õ s ?xative for 24 h.

A serial dehydration process was conducted using increasing concentrations of an alcohol solu- tion to remove excess water from the gonad sample (Khalil 2013). The clearing process was carried out by immersing the gonad specimen in a xylene solution. The gonad sample was then impregnated with paraf?n wax using a tissue embedding sys tem (Leica EG1160) to maintain tissu e integrity and to facilitate cutting by the microtome (Leica RM 2135). Sections were mounted on glass slides, stained with hematoxylin to aid observations and then sealed with a cover slip using DPX glue.

Classi?cation of Gonadal Development Stages The development stages of gonads were identi?ed using the c r i t e r i a d e s cr ib e d b y S u w a n j a r a t e t a l . (2 0 0 9) . B a s e d o n histological examination and microscopic observation, devel- opmental stages were categorized as indeterminate, developing, ripe, or spawning (see Table 1). Preparation of Shell Cross-Sections Shell cross-sections were prepared from a single valve of each animal using the standard method described by Richardson (1987).

T h e v al v e of ea c h a n i ma l wa s m a r k e d i n p e n c i l f r o m the umbo to the ventral margin along the maximum growth line (Fig. 2). Marked valves were embedded in an epoxy resin (a 2:1 Figure 1. Location of Anadara granosa study site in Balik Pulau, Penang Island, West Coast of Peninsular Malaysia. M I R Z A E I E T A L . 70 ratio of epoxy resin to epoxy hardener) for 24 h to protect the valves during cutting and grinding procedures. The valve/resin moldings were then ?xed on a low-speed saw with a diamond-impregnated blade (Buehler Ltd., Lake Bluff, IL). The low speed made it possible to cut the fragile material without fracturing.

The valves were cut through the pencil mark from the umbo to the ventral margin of the shell. Shell sections were polished using sequential grit sandpapers (240, 400, 600, 800 and 1200 Buehler carborundum grits) to remove epoxy resin from the cut surfaces of the valves. The cut valve surfaces were then polished with an aluminum oxide powder on a semi- a u t o m a t i c po l i s h in g m a c h i n e (F O R C I M A T — F O R C I P O L 300–1V). The cut valve was then removed, rinsed in tap water, a n d d r i e d .

Et c h i n g w a s c o n d u c t e d i n a 0 . 1 % s o l u t i o n of hydrochloric acid (HCl) for

1 min so as to leave the aragonite granules that can distort the cross-section image at the surface of the valve section. Growth Pattern Periodicity T h e ex p e r i m e nt w a s d e s i g n e d t o e x a m i n e w h e t h e r t i d a l c h a n g e , em e r s i o n , an d d a i l y r h y t h m s ha d a n y e f f e ct on s h e l l b a n di n g f o r m a t i o n i n A n a d a r a gr a n o s a . T h e t o t a l nu m b e r o f gro wt h ba nds w as co un t ed i n e ach s he l l be tw e en t h e Al i z ar i n r e d s t a i n i n g p o i n t a nd th e s h e l l ma r g i n .

A t - t e s t w a s us e d t o d e t e r m i n e w h e t h e r b a n d n u m b e r w a s a s s o c i a t e d w i t h n um - b e r of da y s , ti d a l p at t e r n s , or em e r s i o n ev e n t s . T h e m e a n di f f er en c e b e t w ee n p a i r s o f e x p ec t e d a n d o b s e r v e d va l u es w a s us ed t o d e t e r m i n e w h e t h e r t h e v a l u e s d i f f e r e d s i g n i ? - ca n t l y f r o m ze r o . Increment Width Measurement The etched shell cross-section was examined under a light stereomicroscope (Olympus SZ61; Olympus Optical Co. Ltd.,

T o k y o , J a p a n) a t 3 1 0 0 m a g n i ? c at i o n a nd p h o t o g r a p h e d (Xcam Alpha; The Imaging Source GmbH). For each sample, microgrowth increments were measured from the shell margin to the Alizarin red staining point using microscopic image TABLE 1. Classi?cation of gonadal development stages in male and female Anadara granosa (Suwanjarat et al. 2009). Gonadal stages Histological characteristics Male Female Indeterminate This stage is also called the inactive stage, during which the sexes cannot be distinguished. In the undeveloped stage, connective tissue can be observed.

There is no trace of gonad development and specimens cannot be sexed visually. In this phase, some residual gametes, which are derived from the gamete release stage, are occasionally found. These gametes will be reabsorbed and there is no progress in development Developing Follicles start to grow, and connective tissue is reduced. Starting from the outer layers to the center, all developmental stages are present, that is, spermatogonia, abundant spermatocytes, smaller spermatids, and ripe spermatozoa with their pink tails.

The average diameter of the follicles at this stage is 117.77 ± 19.58 mm Follicles begin to grow and ?ll with oogonia and developing oocytes (increased size and irregular shapes) associated with the follicular wall. Some ripe oocytes with a large nucleus may be observed free in the lumen. The average diameter of the follicles at this stage is 136.2 ± 22.12 mm and the average diameter of oocytes is 24.81 ± 6.19 m m Ripe Follicles are enlarged and strati?ed. Spermatozoa dominate and are tightly packed in the follicle, whereas spermatogonia are restricted to a thin layer at the periphery of the follicle. Only a small amount of connective tissue is present.

The average diameter of the follicles at this stages is 186.16 ± 14.47 mm Follicles are large, distended, and ?lled with free, polyhedral-shaped, ripe oocytes with a large nucleus and a small nucleolus. The interfollicular space decreases. Few oogonia and immature oocytes remain attached to the follicle wall. The average diameter of the follicles at this stage is 215.13 ± 38.40 mm and the average diameter of oocytes is 30.01 ± 6.80 m m Spawning Gamete release starts. Follicles present small, empty spaces with many free residual spermatozoa. Some follicles have irregular shapes with contracted membranes and a small diameter. Spermatogonia are not found in this stage Oocytes are released from the follicle.

Follicle walls look broken and empty, but still distended. Much residual material is seen. Some types of phagocytes appear in the space between the residual oocytes, which now look rounded F igur e 2. Cuttin g dir ecti on f rom umbo t o ventra l margin alon g the maximum growth line. T EMPORAL V A R I A T I O N I N S HELL G ROWTH R A T E O F A. G R A N O S A 71 an a l ys i s s o f t w a r e (A n al ys i s I m a ge P r o c es s i n g V er s i o n 5. 1; Olympus Soft Imaging Solutions 1989–2008).

Measurement of Environmental Factors D a i l y s e a w a t e r te m p er a t u r e a n d s e a w a t e r s a l i n i t y we r e me asu r ed us i ng a HO BO Pe nd an t Te mp / Lig ht l ogg er an d a hand-held refractometer (RHSN-10ATC BUILT), respec- tively. The logger was calibrated to record hourly seawater temperatures for the 1-y study period and seawater salinity was m e a s u r e d d a i l y a t t h e st u d y s i t e f o r t h e p e r i o d b e t w e e n December 2011 and November 2012. Statistical Analysis To determine the relationship between shell increment width and the reproductive cycle, monthly samples were divided into t w o g r o u p s , na m e l y , a g r o w i n g g r o u p (i n de te r mi n at e a n d developing stages) and a spawning group (ripe and spawning stages). Two-sample independent t-tests were used to compare the means of the increment widths between the growing groups and the spawning groups as well as the means of the increment widths between males and females.

Correlation analysis was used to determine the linear relationship between increment widths in spawning and growing groups with each environmen- tal variable. A P val ue < 0.05 was considered statistically signif- icant and all data are presented as means ± SE. RESULTS Microscopic Description of the Male Gonad In the indeterminate stage, when the gonad was empty and only connective tissue was present, the sexes were indistinguish- able and connective tissue can be observed.

Some residual g a m e t es fo l l ow i ng r el e a s e co u l d b e fo u nd in th e g on a d s (F i g . 3A). The de v el op i n g s t a ge wa s c h ar a c t er iz ed by th e presence of spermatogonia on the follicular wall. Spermatocytes and spermatids were most

abundant, and a number of sperma- toz oa we r e fou nd tow ard the end of the dev elo pin g st age (Fig. 3B). In the ripe stage, follicles were full of spermatozoa, the tails of which were pointed toward the center of the lumen. Only a small amount of connective tissue is present. The average diameter of the follicles at this stages is 186.16 ± 14.47 mm (Fig.

3C). Spermatozoa are released during the spawning stage, leaving an empty space in the follicular lumen. Some follicles have irregular shapes with contracted membranes and a small diameter (Fig. 3D). Microscopic Description of the Ovary The sexes could not be distinguished in the indeterminate stage. At this stage, connective tissue and some residual gametes f o l l o w i n g g a m et i c r e l e a s e c o u l d be f o u n d i n t h e go n a d s (Fig. 4A). During the developing stage, immature oocytes were observed attached to the basal membrane. Various sizes of developing oocytes were found, which possessed basophilic cytoplasm containing irregularly shaped nuclei.

The average diameter of the follicles at this stage is 136.2 ± 22.12 mm and the average diameter of oocytes is 24.81 ± 6.19 m m (Fig. 4B). The size of oocytes increased in the ripe stage. Acidophilic cyto- plasm and yolk granules were clearly visible and ripe oocytes were mostly free in the lumen. The average diameter of the follicles at this stage is 215.13 ± 38.40 m m and the average diameter of oocytes is 30.01 ± 6.80 mm (Fig. 4C). During the spawning stage, the number of ripe oocytes decreased and empty spaces were observed in the follicular lumen. Some types of phagocytes appear in the space between the residual oocytes, which now look rounded (Fig. 4D). Figure 4.

Photomicrograph of a histological section of (A) indeterminate, (B) developing, (C) ripe, and (D) spawning stages of a female gonad in Anadara granosa. FW, follicular wall; Lu, lumen; Ct, connective tissue.; MO, matu re oocyte; LVO, late vitellogeni c oocyte; N, nucleus; IS, interfollicular space; RO, residual oocyte; FF, fragment follicles; EF, empty follicles. Figure 3. Photomicrograph of a histological section of (A) indeterminate, (B) developing, (C) ripe, and (D) spawning stages of a male gonad in Anadara granosa.

FW, follicular wall; Lu, lumen; Ct, connective tissue; MS, mature spermatozoa; St, spermatid; Spz, spermatozoa; D Sz, de- generative spermatozoon. M I R Z A E I E T A L . 72 Reproductive Cycle of Anadara granosa T h e i n d et e r m i n a t e st a g e p r ed o m i n a t e d f o r bo t h se x e s throughout the study period. The percentage of samples in the i n d e t e r m i n a t e s t a ge w a s hi g h e s t i n D e c e m b e r 2 0 1 1 (5 7 %) , followed by August 2012 (54%), November 2012 (54%), June 2012 (40%), and July 2012 (30%), whereas the lowest percent- age was in April 2012 (8%). The developing stage was observed for both sexes through- out the year, with the highest percentages of females at this stage during July 2012 (46%), March 2012 (42%), February 2012 (35%),

and January 2012 (27%).

The frequency of females undergoing this stage was lowest in December 2011 (21%) and November 2012 (21%). A similar trend for the developing stage w a s o bs er v ed f or m al e A na d ar a gr an os a , wi th t h e hi gh e s t frequencies in this stage during January 2012, February 2012, and March 2012 (46%, 37%, and 28% respectively), but with an additional peak in August 2012 (48%). T he max imum freq ue ncy of th e ripe stage in femaleAnada ra g r anosa oc cur red du ring April (57 %), f ollo wed by J anu ary (50%), Februa ry (40 %), a nd M arch (38%).

For male s, t he ripe stage was obse rved with the hig hes t frequency i n Dec ember 2011 (40%) and Februa ry 201 2 (45%). The s pawning s tag e was obs er ve d t hrough- out t he study pe r iod (Dec ember 201 1 t o Novem be r 2012) i n both male and f e male A. gra nosa; however, in female, pe aks in the spa wning period were observed in April 20 12 (1 5%) a nd l ate June (28%).

For males , t he peak spawning pe riod (19 %–44 %) was observe d fr om Ma rch 2012 to late J une 2 012, with a s ec ondary pe ak obs er ve d i n O ctober 2012 (21%) (Fig. 5). Microgrowth Pattern Periodicity The mean numbers of microgrowth bands deposited in the shell layer were almost the same as the total number of tidal e m e r s i o n s i n f o r t n i gh t l y pe r i o d s f r o m D e c e m b e r 2 01 1 t o January 2012. There was no signi?cant difference between the number of observed microgrowth lines and number of tidal emersions for shells in the intertidal area (P > 0.05) (Fig. 6).

However, the number of microgrowth lines during the study period was signi?cantly different from the number of days and t i d a l c h a n g e s f o r s a m p l e s o b t a i n e d f r o m t h e i n t e rt i d a l a r e a (P < 0.05). Shell Increment Width Measurements Th e s h ell in crem ent wid ths o f i ndividuals in the i ndeterminate and de veloping s ta ges (growing group) w e re rela tiv ely stable f rom Dec ember 20 11 to e arly June 2012, ra nging f rom 47 t o 57mm. Figure 5. Distribution of gonadal stages in (A) female and (B) male Anadara granosa in Penang Island, Malaysia (December 2011 to November 2012). T EMPORAL V A R I A T I O N I N S HELL G ROWTH R A T E O F A.

G R A N O S A 73 Shell i nc reme nt widths the n de cre ased t o 35–45m m from early June 2012 to ear ly Sept ember 2012. Increment widths again inc r ease d r anging be twe en 47 and 57m m dur ing t he last 2 m o o f the study period (October to December 2012) (Fig. 7). Throughout the study period, shell increment widths of cockles in the spawning group typically ranged from 8 to 17 mm.

However, during the spawning stage, increment widths de- creased to less than 5 mm

for some individuals, resulting in a spawning break within the shell structure (Fig. 8). Based on gonad histology analysis, gonad maturation progressed from the spawning stage to indeterminate (spent) stage following the s p a w n i n g b r e ak , w i t h t h e in c r e m e n t w i d t h s gr ad u a l l y i nc r ea s - i n g to 47 – 57 m m d u r i n g th e i n de t e r mi nat e a nd d ev e l o p i n g s t a g e s .

T h e in d e p e n d en t s a m p l e (t w o - t a i l e d) t - t e s t s h o w e d t h e r e we r e no si gn i ?c a n t di f f er enc e s b e t w e e n i nc r e me nt wi d t hs o f m al es a n d f e ma l e s in th e s p aw n i n g (P ¼ 0 . 8 2 7) a n d g ro w i n g (P ¼ 0 . 7 9) g r o u p s ; h o w e ve r , t h e r e w a s a s i g n i ? c a nt d i f f e r e n c e b e t w e e n i n c r e m en t wi d t h s in th e s p a w n i n g a nd g r o w i n g g r o up (P < 0 . 0 05) (T ab l e s 2 a n d 3) . Environmental Parameters D a i l y va r i at i o n s i n sea w a t e r t e m p er a t u r e r a n ged f rom a maximum of 33° C to a minimum of 22° C over the course of the study period.

Figure 9A shows the frequent signi?cant ?uctuations in seawater temperature observed during December 2011 and January 2012. Between late January 2012 and late June 2012, seawater temperature remained relatively stable (between 28°C and 33°C) for a period of 3 mo, before increasing to 30°C i n l at e Se pt em be r 20 12. Du r i ng the l as t 2 mo of the s t ud y pe r iod (O c t o b e r a n d N o v e m b e r 2 0 1 2) , t h e te m p e ra t u r e r e m a i n e d r el at iv el y s ta bl e (28– 33 ° C).

I n g e n e r a l , s e a w a t e r s a l i n i t y re m a i n e d re l a t i v e l y st a b l e , r a n g i n g b e t w e e n 2 9 a n d 31 t h r o u g h o u t t h e 1 - y st u d y period (F i g . 9B) . T h r e e p e r i o d s of ?u c t u a t i n g se a w a t e r sa l i n i t y w e r e o b s e r v e d i n D e c em b e r 2 0 1 1 , f r o m A p r i l 2 0 1 2 t o l a t e M a y 2 0 1 2 an d f r o m l a t e S e p t e mb e r 2 0 1 2 t o l a t e N ov e m b e r 2 0 1 2 . S e a w a t e r s al i n i t y d r o p p e d s h a r p l y a n d r e a c h e d t o t h e l o w e s t p o i n t (1 1) on De ce m b e r 1 2 , 2 0 1 1 .

T h e s e c o n d l o w e s t s e a w a t e r s a l i n i t y w a s 1 4 o n M a r c h 6, 2 0 1 2 an d O c t o b e r 2 7 , 2 0 1 2 . Correlation Matrices C o r r e l a t i o ns b et we en in c r em e n t w i d t h s an d en v i r o n me nt a l f a c t o r s (t em pe r a t u r e a n d s a l i n i t y) ar e sh o w n in Ta b l e 4. T he c o r r e l a t i o n m a t r i c e s sh o w e d a s t r on g d i r e c t r el a t i o n s hi p between increment widths in the growing group and temperature Figure 6.

Shell microgrowth pattern formed from 6 to 31 December 2011 for an individual (shell length: 13 mm, age: 5 mo) of Anadara granosa collected from Pinang Island, Malaysia. Figure 7. Shell increment width of the two groups (growing and spawning) of Anadara

granosa, collected from Balik Pulau, Penang Island, Malaysia (December 2011 to November 2012). M I R Z A E I E T A L . 74 (r ¼ 0 . 6 4 2 , P < 0 . 0 5) . T h e r e wa s a w e a k p o s i t i v e co r r e l a t i o n b e t w e e n sa l i n i t y an d i n c r e m e n t w i d th i n t h e gr o w i n g g r o u p (r ¼ 0.46, P < 0 .

0 5) , bu t t h e r e w a s n o c or r e l a t i o n b e t w e e n i n c r e m e n t w i d t h i n t h e sp a w n i n g gr o u p w i t h e i t h e r t e m p e r - a tu r e or sa l i n i t y . DISCUSSION Histological examination of the gonads showed gametogenic activity and indicated that Anadara granosa spawn throughout the year, with a maximum spawning period observed from April to late June. A second peak in spawning occurred in October. Ba s ed on e nv i r o nm en t a l dat a , th e m a i n s p a w n i n g s e a s o n coincided with high seawater temperatures (30–33 ° C) a n d considerable ?uctuations in seawater salinity (14) during the 1-y study period.

Under the optimal conditions of the growing period, the shell increment width ranged from 47 to 57 m m. Shell increment width patterns decreased with decreasing seawater temperature in the study area. In the spawning group, changes i n s he l l in cr em en t w i d t h s w er e m a s k ed by t he im p a c t of spawning activity. A p o s s i b l e e x p l a na t i o n f o r th e d i f f e r e n c es bet w e en i n cr e - me n t w i dt h s i n s p aw ni n g an d gr o w i n g i n d i v i d u al s m i g ht b e ch a ng es in fe ed i ng a ct i v i t y d ur i n g t he spa wn i ng s eas o n. Figure 8. Interior shell section of Anadara granosa showing (A) cessation of growth (spawning break) during the spawning stage and (B) wide microgrowth increment during the developing stage. TABLE 2.

Two-sample independent t -tests between increment widths in males and females of Anadara granosa in growing and spawning groups from December 2011 to November 2012. LeveneÕs test for equality of variances t -test for equality of means F Sig. t df Sig. (two tailed) Growing group Equal variances assumed 0.080 0.77 –0.21 182 0.82 Equal variances not assumed –0.21 181.9 0.82 Spawning group Equal variances assumed 0.43 0.51 0.25 182 0.79 Equal variances not assumed 0.25 181.57 0.79 T EMPORAL V A R I A T I O N I N S HELL G ROWTH R A T E O F A. G R A N O S A 75 C o c k l e s c a n s u d de n l y s t o p f e ed i n g i n t he l at e r i p e an d e ar l y s p a w n i n g s t ag e s (K a n az a w a & S at o 2 0 08).

Th e r ef or e , th e i r gr o w t h r a t e s w o ul d s i g n i ? c a nt l y de c r e a s e d u r i ng sp a w n i n g p er io d . M o r e o v er , r e p r o d u c t i o n i s o n e o f t h e mo s t e n e r g y - c on s u mi n g p h y s i o l o gi ca l a c t i v i t i e s , wi t h g am e t o g en e s i s a c t i n g as a r e gu l at or t h u s e x er t i ng c o n s i d e r ab l e i n? u e n c e o n s h e l l f o r m a t i on .

Consequently, the allocation of energy into gamete release leads to different shell growth rates between spawning and growing groups. This conclusion veri?es the ?ndings of Lewis and Cerrato (1997) who studied the formation of increments and rings in the shell of Myaarenaria and reported that a decline in metabolic activity before the spawning stage was responsible for growth cessation.

Sato (1995) found that a sudden decrease in feeding activity during the ripe and early spawning stages led to a decline in the growth of Phacosoma japonicum shells. Moreover, Miyaji et al. (2007) reported that mollusc species secrete calcium carbonate in their shells at a high rated during their growth period, which necessitates use of almost all of their energy resources. However, due to utilization of energy resources to cover the spawning period, shell increment widths decrease sharply during the spawning stage.

There was a similarity between the spawning period described in this study and those observed in earlier studies (Table 5). Broom (1983) reported that Anadara granosa spawned throughout the year, with a maximum spawning period in October. Similarly, Narasimham (1969) observed year-round spawning in species, but with a period of high intensity from January to April.

Khalil (2013) also reported year-round spawning but with peaks between June and September (Banda Ache, Indonesia), April and October (Lhokseumawe, Indonesia), and June and September (Penang, Malaysia). These peaks are consistent with remarks by Sarkis et al. (2006), who stated that the majority of spawning in tropical species occurred exclusively or most intensely during the warmer months.

In addition, the developing stage predominated during periods of lower temperatures [July to September (28.5 –27° C)]. The histological analysis of the gonads showed that the spawning stage coincided with some frequent strong ?uctua- tions in seawater salinity. This ?nding is in agreement with those of Toral-Barza and Gomez (1985) who reported that a major spawning period for Anadara granosa in the west coast of Malaysia occurred when low salinity continued over a short period (Fig. 9C).

Growth breaks in shell cross-sections of Anadara granosa are formed by an interruption in shell growth. These growth breaks arise from various environmental or physiological

stressors such as temperature or salinity shocks, shell margin abrasions, TABLE 3. Two-sample independent t-tests between increment widths in growing and spawning groups of Anadara granosa from December 2011 to November 2012. LeveneÕs test for equality of variances t -test for equality of means F Sig. t df Sig.

(two tailed) Equal variances assumed 34.47 0.00 –113.80 695 0.000 Equal variances not assumed –114.15 592.63 0.000 F i gu r e 9. Re l a t i on s h ip be t w e e n s p aw ni n g p e r io d a n d e n v i ro n me n t al parameters (temperature and salinity) of Anadara granosa from Penang Island, Malaysia (December 2011 to November 2012). (A) Daily seawater temperature; (B) daily salinity; (C) spawning frequency. TABLE 4. Correlation matrix between increment widths in growing and spawning groups of Anadara granosa and environmental factors.

Temperature Salinity Increment width (mature group) Temperature 1 0.29 0.642 Salinity 0.29 1 0.46 Increment width (growing group) 0.642 0.46 1 Temperature Salinity Increment width (immature group) Temperature 1 0.29 0.420 Salinity 0.29 1 0.304 Increment width (spawning group) 0.310 0.204 1 M I R Z A E I E T A L . 76 s p aw ni ng , s p ri n g ti de s, an d/ or s t ro ng cu rr en ts (T ho mp s o n et al. 1980, Sch €one et al. 2005). A possible means to distinguish s pa wn i n g b r ea ks fr om oth er t y pe s of g r owth b r ea ks is she l l incr ement width characteristics. In the present study, increment widths quickly decreased to less than 5m m b efore a spawning break.

A f t e r t h e s p a w n i n g b r e ak , w h e n t h e i n di v i d u a l s w e r e i n i n d et e r m i n a t e an d d ev e l o p i n g s t a g e s , t h e i n c r e m e n t w i d t h s g r a d u a l l y i n c r e a s e d to 4 7 – 5 7 mm . I n a d d i t i o n, ba s e d o n h i s t o l o g i c a l a n a l y s i s , i t w a s o b v i o u s t h a t gr o w t h br e a ks i n t h e cu r r e n t s t u d y w e r e f o r m ed i m m e d i a t e l y b e f o r e s p a wn i n g , w h e n t h e go n a d s w e r e st i l l ? l l e d with sperm and free oocytes; h o w e v e r , a c c o r d i n g to S a t o (1 9 9 5) , f o r i n d i v i d u a l s w h o s e g r o w t h b r e a k w a s f o r m e d d u e t o e n v i r o n m e n t a l s t r e s s , i n c r e - m e n t w i d t h ra p i d l y i n c r e a s ed af t e r t h e g r o w t h b r e a k w i t h i n t h e sh e l l c r o s s se c t i o n .

T h e r e s u l t s ar e i n a gr e e m e n t w i t h K a n a z a w a a nd Sa t o (2 0 0 8) ? n d i n g s , w h i c h s h o w e d wi d e l y s p a c e d g r o w t h i n c r e m e n t s c e a s es s u d d e n l y be f o r e s p a w n i n g , a n d af t e r sp a w n i n g , t h e gr o w th i n c r em e n t s gr a d u a l l y i n c r e a se i n w i d t h a s gr o w t h re c o v e r s . This study has shown that microincrements in shell width of cockles provide a precise indication of the timing of gonad maturity stages.

Shell increment width analysis also showed spawning breaks, which are considered

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