



ORIGINAL ARTICLE

Variation in biochemical composition during gonad maturation of the tropical abalone *Haliotis varia* Linnaeus 1758 (Vetigastropoda: Haliotidae)

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Abstract

Biochemical changes in the body components during gonad maturation of the tropical abalone *Haliotis varia* were investigated using wild collected specimens from the Gulf of Mannar, on the southeast coast of India. The gonadosomatic index (GSI) and the hepatosomatic index (HSI) showed negative correlations throughout the study period as well as during the progression of gonad maturation stages. The highest GSI for both the sexes were in the ripe stages followed by late maturing stages. The HSI ranged from 2.97 to 6.71 in females, and 3.55 to 5.09 in males. Among the biochemical components analysed, lipid and carbohydrate contents showed significant variations in the different tissues of *H. varia* during the progress of gonad maturation. The highest protein content was in the foot muscle and the lowest was in the digestive gland. Total lipids in the ovary were always higher compared with that of the testis and the values ranged from 12.60 to 26.49%, registering the highest value in the ripe ovary. Gonad carbohydrate content was lower when the lipid content was higher, suggesting the conversion of carbohydrate to lipids. The present study demonstrates the role of nutrient translocation between body parts as an essential part of the reproductive physiology of abalone.

Key words: Biochemical changes, gonadosomatic index, *Haliotis varia*, proximate composition, tropical abalone

Introduction

Reproductive changes in marine invertebrates are often associated with translocation of some of the biochemical constituents between somatic tissue and reproductive organs (Giese 1959, 1969). In this perspective, variation in the biochemical composition of the whole body as well as in individual organ systems during different stages of gonad development and maturation are taken into consideration in determining annual reproductive cycles (Giese & Pearse 1974). The basic metabolic levels of various biochemical components in prosobranch molluscs are very high lipid levels and low polysaccharide levels in the gonad and high polysaccharide and low lipid levels in muscular tissue, particularly in the foot. High gonad lipid levels, chiefly in ovaries, have been described in *Haliotis* species (Albrecht 1923; Giese 1966; Webber 1967), and these form the energy source for the egg yolk.

In spite of the procedural complexity in separating the gonad tissues from the rest of the body, considerable information exists on the gonadal biochemistry of bivalves, especially oysters. Many of the pioneering works on oysters have been reviewed by Galtsoff (1964). In contrast to the voluminous studies on oysters and other lamelli-branches, biochemical studies on gastropods are limited. Some of the available literature elucidates various aspects of the biochemical composition of limpets (Barry & Munday 1959; Blackmore 1969), snails (Giese 1967; Oates et al. 1990; Carasco et al. 2006) and abalone (Mercer et al. 1993; Knauer et al. 1994; Chiou et al. 2001, 2002; Litaay & De Silva 2003). Chemical investigations of abalone body components, especially the biochemical composition of foot muscle and its texture properties (Hatae et al. 1995) are of great significance because of their high commercial value in the international market (Guo et al. 1999).

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Although the tropical abalone are smaller in size, recent years have seen an increasing interest in the development of their culture in some Asian countries (Jarayabhand et al. 1995; Jarayabhand & Paphavasi 1996; Najmudeen & Victor 2004a). This is mainly due to the increasing demand for small, live abalone in the markets of Hong Kong and Japan (Guo et al. 1999). Furthermore, the valuable abalone resources have been continuously exploited for its ornamental shells and meat in many Asian countries. In India, abalone are represented by only one species, *Haliotis varia* L., which was reported as early as 1917 (Hornell 1917). The distribution of *H. varia* in the country is limited and restricted to the Gulf of Mannar and Andaman and Nicobar Islands. Several studies have been conducted recently on the reproduction and seed production of *H. varia* (Najmudeen et al. 2000; Najmudeen & Victor 2004a, b). The present investigation was undertaken with the objective to elucidate the movement of biochemical components between tissues during the gonad maturation of *H. varia* from the Gulf of Mannar, on the southeast coast of India.

Material and methods

Collection of abalone

Random live samples of *H. varia* were collected monthly from the intertidal rocks at Tuticorin Harbour basin in the Gulf of Mannar from a depth of 1–3 m during January 1998 to February 1999. The abalone transported to the laboratory were stocked in a 1.5 tonne capacity FRP tank with filtered seawater and kept overnight to allow the clearance of waste materials accumulated in their body. A minimum of 45 specimens were then shucked and dissected to examine the gonad. The soft body weight, gonad weight and digestive gland weight were measured on a wet weight basis. The testis and ovary were classified into six stages each based on the morphological characters of the gonad as well as the presence of gametes, as suggested by Wood & Buxton (1996). The maturity stages identified in both sexes of *H. varia* were (I) early maturing, (II) late maturing, (III) ripe, (IV) partially spawned, (V) spent and (VI) indeterminate (Najmudeen & Victor 2004b).

Gonad and hepatic indices

The measurement of the gonad index as a measure of reproductive cycle is based on the assumption that maturation and breeding coincide with the maximum gonad weight. The gonadosomatic index (GSI) for each abalone was calculated using the formula: $GSI = (\text{wet weight of gonad in grams}/\text{soft body weight of abalone in grams}) \times 100$ (Webber & Giese 1969).

Similarly, the hepatosomatic index (HSI) was calculated using the formula: $HSI = (\text{wet weight of whole digestive gland in grams}/\text{soft body weight of abalone in grams}) \times 100$. Both the GSI and the HSI were calculated for the monthly samples as well as for different maturity stages.

Biochemical analysis

The biochemical composition of foot muscle, digestive gland and gonad of male and female *H. varia* at different maturity stages was analysed using standard analytical procedures. After determining the moisture content of each tissue by gradually dehydrating in a hot air oven at 70°C, the dried samples were used for the estimation of protein, carbohydrate and lipid by spectrophotometric methods on a dry weight basis. Protein was estimated by the Folin-Ciocalteu method (Lowry et al. 1951), carbohydrate by the phenol sulphuric acid method (Dubois et al. 1956) and lipid by the sulpho-phospho vanillin method (Barnes & Blackstock 1973). The ash content was determined by burning the samples for 12 h in a muffle furnace at 550°C. Analyses were performed on 10 samples of tissues from each maturity stage and were done in triplicate.

Statistical analysis

Differences in the GSI and the HSI for males, females and pooled sexes over time and between maturity stages were compared using two-factor analysis of variance (ANOVA) (Snedecor & Cochran 1967). To see if there were significant differences in biochemical constituents between maturity stages, these data were also tested with one-factor ANOVA. Having demonstrated a significant difference within the groups by ANOVA, the Tukey test was applied, to determine where those differences were. Pearson's correlations were carried out between biochemical components and the GSI; and between the GSI and the HSI.

Results

Gonad and hepatic indices

The GSI values varied significantly between months ($P < 0.05$) and between maturity stages ($P < 0.01$) throughout the study period (Figure 1). The highest pooled GSI values were observed in January 1999 (12.33) followed by February 1999 (10.85) and February 1998 (8.97). High values of the GSI were maintained from January to April. A gradual decrease was recorded from March to June 1998, i.e. from the post-monsoon period to summer, which indicates the onset of spawning. The lowest GSI corresponded to August 1998 (2.78) followed by

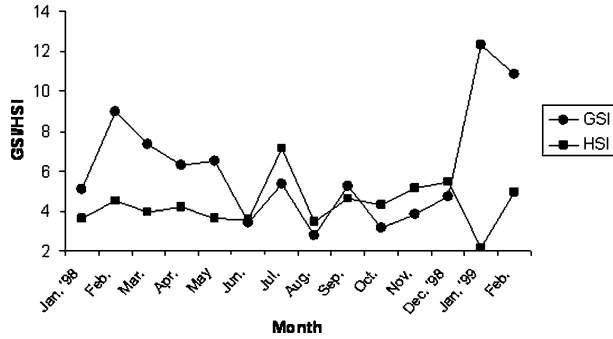


Figure 1. Seasonal changes in the mean pooled gonadosomatic index and the hepatosomatic index of the tropical abalone *Haliotis varia* sampled from the Gulf of Mannar during January 1998 to February 1999 showing their inverse relationship.

October 1998 (3.25). This suggests that the breeding season of *H. varia* at Tuticorin coincides with the post-monsoon period (December–February).

The percentage occurrences of different maturity stages for both male and female *H. varia* are presented in Figure 2(a, b). The highest values of the GSI for both sexes were recorded for individuals in the ripe stages followed by those in late maturing stages. The lowest GSI value was recorded for abalone in the indeterminate stage gonad (1.99). The mean GSI for males ranged from 3.29 (stage I) to 11.03 (stage III) and that of females ranged from

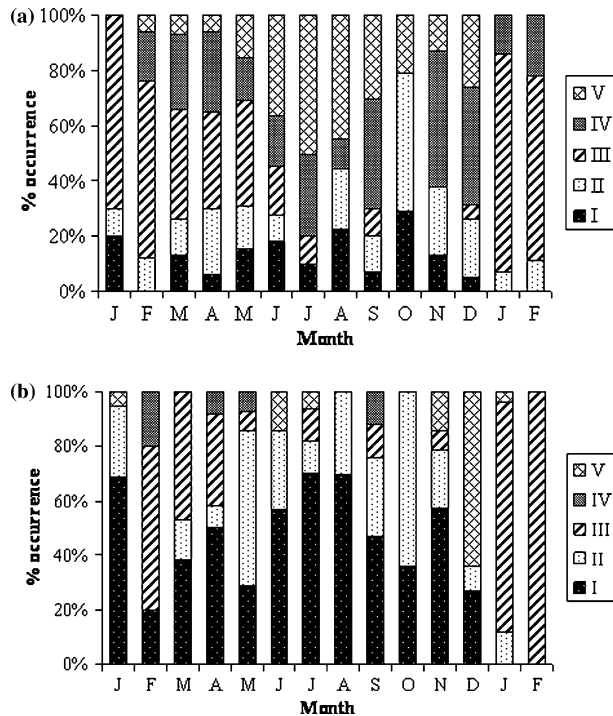


Figure 2. Seasonal changes in gonad maturation stages (I–V) of *Haliotis varia* from the Gulf of Mannar during January 1998 to February 1999, expressed as a percentage occurrence of the total number sampled each month throughout the study period: (a) male, (b) female.

2.74 (stage V) to 10.64 (stage III). In all the maturity stages, the GSI values were consistently higher for females than for males.

The HSI also varied significantly between months, as well as between maturity stages in both sexes ($P < 0.05$). The digestive gland of *H. varia* lies under the gonad and forms a part of the conical appendage. There was a negative correlation between the HSI and the GSI in both sexes (Figure 3a, b). The HSI was lowest when the GSI was highest, i.e. in the ripe stage. The mean HSI values ranged from 2.97 to 6.71 in females, and 3.55 to 5.09 in males.

Biochemical composition

Among the biochemical components analysed, the lipid and carbohydrate content in the different tissues of *H. varia* showed variations during the progress of gonad maturation. In the foot muscle, the moisture content was higher in the indeterminate stage (75.66%). In females, it ranged from 70.09% in stage IV to 73.33% in stage V. In males, water content ranged between 71.33% in stage IV and 75.38% in stage III. The average moisture content in the foot muscle was significantly higher in males than in females. The protein content in the foot

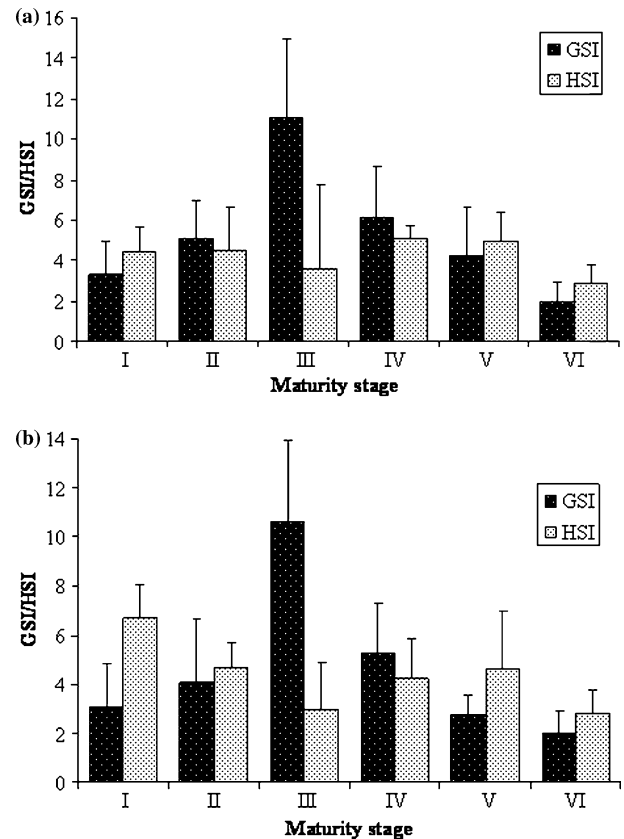


Figure 3. Variation in the gonadosomatic index and the hepatosomatic index at different maturity stages of *Haliotis varia* from the Gulf of Mannar: (a) male, (b) female.

muscle changed through the maturity stages from 68.11 to 74.55% in females and 65.84 to 75.35% in males (Table I). Among the various tissues analysed, the highest protein content (76.39%) was in the foot muscle of abalone with indeterminate stage gonad. The lipid content ranged from 4.10% (stage I) to 6.62% (stage III) in females, whereas males showed a wider range of 2.63% in stage V and 5.80% in stage IV. The lowest value of carbohydrate content was recorded in the indeterminate stage and the fluctuation of carbohydrate during gonad maturation was significantly higher in male foot muscle ($F_{5,30} = 121.28$; $P < 0.05$) than in that of females ($F_{5,30} = 45.10$; $P < 0.05$). In females, the values ranged from 1.98% in stage I to 5.87% in stage IV, and in males, the range was between 0.27% in stage I and 11.18% in stage IV. Variation in ash content in the foot muscle did not show any regular trend compared with all other parameters. It ranged from 6.02 to 6.84% in females and 6.22 to 7.82% in males.

The moisture and protein content in the digestive gland were quite low when compared with that of the foot muscle and gonad tissue (Table II). The moisture content ranged from 51.55 to 68.92% in females and 64.00 to 74.29% in males. In females, the lowest level of protein was in stage V (52.36%) and the highest was in stage II (60.58%), and for males were in stage IV (49.36%) and stage V (55.41%), respectively. The lipid levels in male digestive glands showed a gradual increase as the gonad matured and the highest value observed was in the ripe stage (15.07%). Lipids then decreased gradually and the lowest value was registered in stage VI. In females, the trend was not regular, and the highest value of lipid in the digestive gland was recorded at the spent stage. Carbohydrate values ranged from 9.56 to 15.67% in females, and 6.88 to 11.27% in males. High values of ash content were found in the spent stage of both males and females.

Total lipids in the female gonad were always higher when compared with those of the male gonad (Table III). In females, the lipid content ranged from 12.60 to 26.49% registering the highest value in the ripe gonad. Even though the variation in protein content in the ovary was not significant ($P > 0.05$), a negative correlation was obvious ($r = -0.607$; $P < 0.05$) between the protein content and the GSI (Figure 4). In contrast, there was a positive correlation ($r = 0.866$; $P < 0.05$) between the ovary lipid values and the GSI of the female abalone (Figure 5). There was also a negative relationship between lipid and carbohydrate content in the gonad, especially in the ovaries. The highest value of carbohydrate was in the indeterminate stage of the gonad (4.88%), whereas the highest ash content was in the spent ovary (12.06%).

Table I. Changes in the proximate composition (mean \pm SE) of male and female foot muscle of *Haliotis varia* at different maturity stages. Protein, total lipids, carbohydrate and ash are given in dry weight basis (mg/100 mg of tissue). Values in each column with the same superscripts are not significantly different ($P > 0.05$).

Maturity stage	Male					Female				
	Moisture (%)	Protein	Lipid	Carbohydrate	Ash	Moisture (%)	Protein	Lipid	Carbohydrate	Ash
I	72.34 \pm 3.15 ^{ab}	74.50 \pm 4.29 ^{bc}	5.25 \pm 0.10 ^c	0.27 \pm 0.15 ^a	6.76 \pm 0.41 ^a	71.29 \pm 2.45 ^a	73.57 \pm 3.26 ^b	4.10 \pm 0.83 ^b	1.97 \pm 0.70 ^a	6.83 \pm 1.25 ^{ab}
II	75.36 \pm 3.45 ^b	75.35 \pm 3.12 ^c	3.35 \pm 0.02 ^b	2.88 \pm 0.51 ^b	6.52 \pm 0.54 ^a	72.13 \pm 3.64 ^{ab}	68.11 \pm 2.85 ^a	4.86 \pm 0.52 ^b	0.98 \pm 0.52 ^a	6.63 \pm 0.85 ^{ab}
III	75.38 \pm 1.50 ^b	71.06 \pm 3.67 ^b	5.20 \pm 0.22 ^c	5.65 \pm 1.26 ^c	6.22 \pm 0.52 ^a	72.56 \pm 3.42 ^{ab}	70.35 \pm 3.97 ^{ab}	6.62 \pm 2.89 ^c	4.53 \pm 1.70 ^{bc}	6.58 \pm 0.85 ^a
IV	71.33 \pm 1.85 ^a	65.84 \pm 3.13 ^a	5.80 \pm 1.21 ^c	11.18 \pm 3.89 ^d	6.82 \pm 1.43 ^{ab}	70.09 \pm 4.25 ^a	74.55 \pm 7.40 ^{abc}	5.37 \pm 0.81 ^b	5.87 \pm 0.85 ^c	6.26 \pm 0.43 ^a
V	75.25 \pm 2.85 ^b	69.13 \pm 5.03 ^{ab}	2.63 \pm 0.10 ^a	4.18 \pm 1.51 ^c	7.82 \pm 1.48 ^{bc}	73.33 \pm 2.30 ^b	72.47 \pm 2.48 ^b	4.91 \pm 0.92 ^b	2.26 \pm 0.20 ^{ab}	6.02 \pm 0.87 ^a
VI	75.66 \pm 3.36 ^b	76.39 \pm 3.73 ^c	2.64 \pm 0.29 ^{ab}	1.79 \pm 0.42 ^{ab}	6.63 \pm 0.46 ^a	75.66 \pm 3.26 ^{bc}	76.39 \pm 5.29 ^{bc}	2.64 \pm 0.61 ^a	1.79 \pm 0.42 ^a	6.63 \pm 0.65 ^{ab}

Table II. Changes in the proximate composition (mean \pm SE) of male and female digestive gland of *Haliotis varia* at different maturity stages. Protein, total lipids, carbohydrate and ash are given in dry weight basis (mg/100 mg of tissue). Values in each column with the same superscripts are not significantly different ($P > 0.05$).

Maturity stage	Male						Female					
	Moisture (%)	Protein	Lipid	Carbohydrate	Ash	Moisture (%)	Protein	Lipid	Carbohydrate	Ash		
I	70.24 \pm 1.50 ^b	53.80 \pm 6.25 ^a	8.72 \pm 0.97 ^a	9.88 \pm 2.52 ^{ab}	13.15 \pm 0.35 ^{ab}	61.54 \pm 2.29 ^a	48.67 \pm 4.95 ^a	15.47 \pm 1.45 ^c	13.34 \pm 2.06 ^b	14.63 \pm 0.53 ^b		
II	74.29 \pm 2.72 ^{bc}	55.17 \pm 2.37 ^b	11.65 \pm 1.28 ^b	10.65 \pm 1.45 ^{ab}	12.63 \pm 0.33 ^a	63.25 \pm 1.96 ^b	60.58 \pm 2.86 ^c	12.86 \pm 0.37 ^b	11.02 \pm 2.42 ^{ab}	9.83 \pm 0.37 ^a		
III	66.83 \pm 3.27 ^a	52.18 \pm 5.18 ^{ab}	15.07 \pm 3.14 ^c	11.27 \pm 1.86 ^b	14.06 \pm 1.28 ^{ab}	64.44 \pm 2.16 ^b	53.30 \pm 7.73 ^b	16.51 \pm 2.89 ^d	15.67 \pm 5.74 ^b	12.53 \pm 0.38 ^{ab}		
IV	64.00 \pm 2.93 ^a	49.36 \pm 2.94 ^a	9.13 \pm 1.14 ^a	10.34 \pm 1.38 ^{ab}	13.78 \pm 2.47 ^{ab}	68.92 \pm 1.40 ^c	53.81 \pm 11.04 ^b	16.03 \pm 1.15 ^d	11.64 \pm 1.05 ^{ab}	13.87 \pm 0.51 ^b		
V	67.09 \pm 2.69 ^{ab}	55.41 \pm 8.53 ^b	10.67 \pm 1.30 ^{ab}	6.89 \pm 1.95 ^a	16.79 \pm 3.49 ^b	59.55 \pm 2.98 ^a	52.36 \pm 2.11 ^b	17.41 \pm 1.67 ^d	9.57 \pm 0.69 ^a	14.26 \pm 1.33 ^b		
VI	66.66 \pm 3.67 ^a	50.41 \pm 3.32 ^a	8.26 \pm 2.07 ^a	13.53 \pm 2.85 ^c	12.04 \pm 1.82 ^a	66.66 \pm 1.67 ^{bc}	50.41 \pm 1.34 ^a	8.26 \pm 2.07 ^a	13.53 \pm 2.85 ^b	12.04 \pm 0.82 ^a		

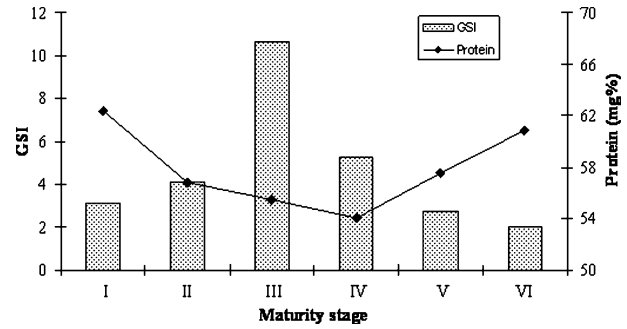


Figure 4. Variation in the gonadosomatic index and gonad protein content of female *Haliotis varia* showing their negative relationship.

Discussion

Abalone, which exhibits broadcast spawning behaviour, allocates much of their metabolic energy during the reproductive cycle for the production of gametes (Giese 1959). The digestive gland cross-section area of abalone usually remains constant throughout the year as compared with the gonad section area, which fluctuates from month to month according to their annual reproductive cycle. However, many studies have reported that the digestive gland will increase in size corresponding to the decrease in the size of the gonad, suggesting that material might be transported from the digestive gland to the gonad (Booolootian et al. 1962; Litaay & De Silva 2003). Such transfer of nutrients from storage or digestive sites to the gonad has been inferred or demonstrated in a number of other groups of molluscs, including bivalve species (Ansell 1974; Gabbott 1975; Le Pennec et al. 1991). Although successful gamete production relies on such transfers, very little is known about the underlying pathways and mechanisms. In the present study, the Pearson correlation showed a significant inverse relationship between the GSI and the HSI, both seasonally and between gonad maturation stages. Litaay & De Silva (2003) reported that the digestive gland of the blacklip abalone *H. rubra*

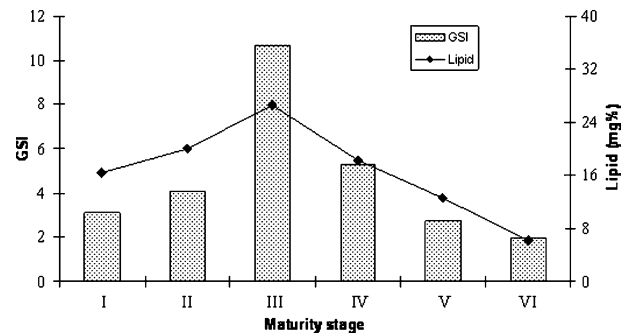


Figure 5. Variation in the gonadosomatic index and gonad lipid content of female *Haliotis varia* showing their positive relationship.

Table III. Changes in the proximate composition (mean ± SE) of male and female gonad of *Haliotis varia* at different maturity stages. Protein, total lipids, carbohydrate and ash are given in dry weight basis (mg/100 mg of tissue). Values in each column with the same superscripts are not significantly different ($P > 0.05$).

Maturity stage	Male				Female			
	Moisture (%)	Protein	Lipid	Ash	Moisture (%)	Protein	Lipid	Ash
I	75.54 ± 2.05 ^b	61.11 ± 6.01 ^b	9.15 ± 0.10 ^b	3.76 ± 2.10 ^{ab}	61.54 ± 2.25 ^a	62.42 ± 5.48 ^{bc}	16.36 ± 1.27 ^c	5.51 ± 0.56 ^b
II	77.23 ± 3.94 ^{bc}	64.75 ± 2.90 ^c	5.53 ± 0.16 ^a	3.68 ± 0.30 ^{ab}	62.46 ± 1.46 ^a	56.79 ± 4.69 ^{ab}	20.01 ± 0.90 ^{cd}	7.73 ± 0.39 ^c
III	74.03 ± 5.05 ^{ab}	64.33 ± 3.40 ^{bc}	9.84 ± 1.69 ^b	4.23 ± 0.65 ^b	63.35 ± 2.58 ^{ab}	55.45 ± 4.97 ^a	26.49 ± 4.64 ^d	4.77 ± 0.54 ^b
IV	70.94 ± 4.74 ^a	54.92 ± 2.39 ^a	10.11 ± 1.58 ^b	1.74 ± 0.36 ^a	66.82 ± 1.64 ^b	54.06 ± 6.63 ^a	18.36 ± 0.93 ^c	2.15 ± 0.60 ^a
V	78.74 ± 6.37 ^c	60.31 ± 4.28 ^b	5.25 ± 1.06 ^a	2.24 ± 0.48 ^a	71.43 ± 2.09 ^c	57.56 ± 3.79 ^{ab}	12.60 ± 0.78 ^b	1.83 ± 0.43 ^a
VI	74.23 ± 3.05 ^{ab}	60.82 ± 3.46 ^b	6.15 ± 0.94 ^{ab}	4.88 ± 0.70 ^b	74.23 ± 1.05 ^c	60.82 ± 3.56 ^b	6.15 ± 0.94 ^a	4.88 ± 0.70 ^b

acts a nutrient store, and as maturation proceeds nutrients are drawn from the digestive gland, resulting in the lowering of the HSI. The negative relationship of the GSI and the HSI in *H. varia* can be further explained by the variation in some of the biochemical constituents, especially protein and lipid in the gonad as well as in the digestive gland. For example, the protein content in the female digestive gland decreased considerably in the ripe stage, indicating the utilization of protein from the digestive gland for some purposes related to ovarian maturation. In gastropods, ferritin is an important component of yolk (Fioroni & Schmekel 1976). In most species, the only extra gonadal protein accumulated in yolk granules is ferritin. This protein is reported to be derived from the digestive gland (Heneine et al. 1969). Ovarian lipid content also increases as maturation advances and declines gradually towards the spent stage.

Among all the tissues analysed, the highest value of protein was observed in the foot muscle of *H. varia*, as noted in most bivalves and gastropods, and it is a little higher than that of the other abalone species reported (Litaay & De Silva 2003). Previous studies have reported that much of the energy resources of molluscs are stored in the foot muscle (Pazos et al. 1997; Berthelin et al. 2000) and the digestive gland (Sastry & Blake 1971; Berthelin et al. 2000). Furthermore, earlier studies have also shown that the digestive gland is implicated not only in nutrient storage but also in the transfer of assimilated food to body tissues in molluscs (Sastry & Blake 1971). The irregular trend observed in the foot protein content in *H. varia* might be due to its involvement in growth and metabolism rather than in reproduction, as concluded by Giese et al. (1967) for the pismo clam *Tivela stultorum*, in which monthly variations in protein level had no relation to the reproductive season, but rather were related to nutrient conditions and other variables in the environment. Among the three tissues analysed, the digestive gland of *H. varia* contained the lowest level of proteins. This low level of protein is balanced by the presence of high levels of lipid and carbohydrate compared with that of the foot muscle.

The positive correlation between the lipid content of the ovary and the GSI of *H. varia* is probably associated with the process of vitellogenesis. The highest value of lipid among all the tissues was in the ripe ovary (26.49%). In *H. rubra*, the gonad lipid content was as high as 40.4% during the peak breeding season (Litaay & De Silva 2003). During oogenesis and spermatogenesis there is a rapid increase in lipid and protein in the gonad, as reported for scallop (Barber & Blake 1991) and oyster (Soudant et al. 1996). However, in *H. varia*,

in contrast to the lipid levels, protein content did not show such an increase in the ripe stage of ovary, instead it recorded a decline compared with that of the preceding stages. Moreover, the gonad lipid levels followed the pattern described for other molluscan broadcast fertilisers in that ovary lipid levels were about twice the testis lipid levels (Giese 1967; Litaay & De Silva 2003).

Another significant observation made during the present study was the inverse relationship between carbohydrate content and lipid levels in some of the organs of *H. varia*. For instance, the gonad carbohydrate content was lower when the lipid content was higher. Many of the previous studies in bivalves have reported such correlations. Tanaka & Hatano (1952) have shown that in lamellibranch gonad as lipid levels rise, glycogen levels decrease. In *Crassostrea gigas* (Hatanaka 1940) and *Pinctada martensi* (Ashikaga 1948), it was reported that carbohydrate was converted to lipid during gametogenesis. A similar synchrony of glycogen breakdown and vitellogenesis has been recorded for *Mytilus edulis* by Gabbott & Bayne (1973).

The translocation of biochemical components between body components is an essential part of the reproductive physiology of molluscs, and this has been further demonstrated by the present investigation. As in many other species of abalone, the digestive gland plays a major role in supplying nutrients for the gonad maturation process in *H. varia*. Apart from the role in determining the annual reproductive cycle of this valuable species in the country, the investigation on the biochemical changes in various tissues at different stages of maturation may provide an insight into nutritional requirements, which forms the baseline information to formulate adequate diets for their cultivation.

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References

Albrecht PG. 1923. Chemical study of several marine molluscs, reproductive system. *Journal of Biological Chemistry* 56: 395–405.

- Ansell AD. 1974. Seasonal changes in the biochemical composition of the bivalve *Chlamys septemradiata* from the Clyde Sea area. *Marine Biology* 25:85–99.
- Ashikaga C. 1948. Biochemical studies on the pearl oyster, *Pinctada martensi*. I. The seasonal variations of the chemical composition especially glycogen content. *Seiri Seitai* 2:60–167.
- Barber BJ, Blake NJ. 1991. Reproductive biology. In: Shumway SE, editor. *Scallops: Biology, Ecology and Aquaculture*. Amsterdam: Elsevier. p 378–428.
- Barnes H, Blackstock J. 1973. Estimation of lipids in marine animals and tissues: detailed investigation of the sulphophosphovanillin method for total lipids. *Journal of Experimental Marine Biology and Ecology* 12:103–18.
- Barry RJC, Munday KA. 1959. Carbohydrate levels in *Patella*. *Journal of the Marine Biological Association of the United Kingdom* 38:81–95.
- Berthelin C, Kellner K, Mathieu M. 2000. Storage metabolism in the Pacific Oyster (*Crassostrea gigas*) in relation to summer mortalities and reproductive cycle (West Coast France). *Comparative Biochemistry and Physiology* 125:359–69.
- Blackmore. 1969. Studies on *Patella vulgata*. II. Seasonal variation in biochemical composition. *Journal of Experimental Marine Biology and Ecology* 3:213–45.
- Booolootian RA, Fermafarmaian A, Giese AC. 1962. On the reproductive cycle and breeding habits of two western species of *Haliotis*. *Biological Bulletin of the Marine Biology Laboratory, Woods Hole* 122:183–93.
- Carasco CA, Navarro JM, Leiva GE. 2006. Biochemical composition and tissue weight of *Chorostoma giganteus* (Gastropoda: Muricidae) exposed to different diets and temperature during reproductive conditioning. *Interciencia* 68:380–7.
- Chiou TK, Lai MM, Lan HM, Shiao CY. 2002. Extractive component changes in the foot muscle of live small abalone during storage. *Fisheries Science* 68:380–7.
- Chiou TK, Lai MM, Shiao CY. 2001. Seasonal variations of chemical constituents in the muscle and viscera of small abalone fed different diets. *Fisheries Science* 67:146–56.
- Dubois M, Giller KA, Hamilton JK, Robers RA, Smith F. 1956. Calorimetric method for determination of sugars and related substances. *Analytical Chemistry* 28:350–6.
- Fioroni P, Schmekel L. 1976. Die nahrungsfreie Gastropoden-Ontogenese. *Ontogenese of Gastropods with rich nutritive resources. Zoology Jb Abt Anatomy* 96:74–171.
- Gabbott PA. 1975. Storage cycles in marine bivalve molluscs: a hypothesis concerning the relationship between glycogen metabolism and gametogenesis. In: Barnes H, editor. *Proceedings of the 9th European Marine Biological Symposium*. Aberdeen: University Press. p 191–211.
- Gabbott PA, Bayne BL. 1973. Biochemical effects of temperature and nutritive stress on *Mytilus edulis* L. *Journal of the Marine Biological Association of the United Kingdom* 53:269–86.
- Galtsoff PS. 1964. The American oyster: *Crassostrea virginica*. *Fisheries Bulletin of the Wildlife Service US* 64:1–480.
- Giese AC. 1959. Annual reproductive cycles of marine invertebrates. *Annual Review of Physiology* 21:547–76.
- Giese AC. 1966. Lipids in the economy of marine invertebrates. *Physiological Reviews* 46:244–98.
- Giese AC. 1967. Some methods for the study of the biochemical constitutions of marine invertebrates. *Oceanography Marine Biology Annual Reviews* 5:159–86.
- Giese AC. 1969. A new approach to the biochemical composition of the mollusc body. *Oceanography Marine Biology Annual Reviews* 7:115–29.
- Giese AC, Hart MA, Smith AM, Cheung MA. 1967. Seasonal changes in body component indices and biochemical composition in the Pismo clam, *Tivela stultorum*. *Comparative Biochemistry and Physiology* 22:549–61.

- Giese AC, Pearse JS. 1974. Introduction: general principles. In: Giese AC, Pearse JS, editors. *Reproduction of Marine Invertebrates* Vol. 1. New York: Academic Press. p 1–49.
- Guo X, Ford SE, Zhang F. 1999. Molluscan aquaculture in China. *Journal of Shellfish Research* 18:19–31.
- Hatae K, Nakai H, Shimada A, Murakami T, Takada K, Shirojo Y, Watabe S. 1995. Abalone (*Haliotis discus*): seasonal variations in chemical composition and textural properties. *Journal of Food Science* 60:32–9.
- Heneine JF, Gazzinelli G, Tafuri WL. 1969. Iron metabolism in the snail *Biomphalaria glabrata*: uptake, storage and transfer. *Comparative Biochemistry and Physiology* 28:391–9.
- Hornell J. 1917. The edible molluscs of the Madras Presidency. *Madras Fisheries Bulletin Report No: 1* 11:1–51.
- Jarayabhand P, Kojima H, Menasveta P. 1995. Embryonic and larval development of abalone, *Haliotis ovina* Gmelin. *ARRI Newsletter* 2:9–15.
- Jarayabhand P, Paphavasit N. 1996. A review of the culture of tropical abalone with special reference to Thailand. *Aquaculture* 140:159–68.
- Knauer J, Hecht T, Duncan JR. 1994. Proximate composition of the South African abalone, *Haliotis midae* (Haliotidae: Gastropoda). *Aquaculture and Fish Management* 25:351–4.
- Le Pennec M, Beninger PG, Dorange G, Paulet YM. 1991. Trophic sources and pathways to the developing gametes of *Pecten maximus* (Bivalvia Pectinidae). *Journal of the Marine Biological Association of the United Kingdom* 71:451–63.
- Litaay M, De Silva SS. 2003. Spawning season, fecundity and proximate composition of the gonads of wild-caught blacklip abalone (*Haliotis rubra*) from Port Fairy waters, south eastern Australia. *Aquatic Living Resources* 16:353–61.
- Lowry OH, Roseborough NJ, Farr AL, Randall RJ. 1951. Protein measurement with the Folin phenol Reagent. *Journal of Biological Chemistry* 193:265–75.
- Mercer JP, Mai KS, Donlon J. 1993. Comparative studies on the nutrition of two species of abalone, *Haliotis tuberculata* Linnaeus and *Haliotis discus hannai* Ino. I. Effects on algal diets on growth and biochemical composition. *Invertebrate Reproduction and Development* 23:75–88.
- Najmudeen TM, Ignatius B, Victor ACC, Chellam A, Kandasami D. 2000. Spawning, larval rearing and production of juveniles of the tropical abalone *Haliotis varia* Linn. *Marine Fisheries Information Service Technical and Extension Series* 163:5–8.
- Najmudeen TM, Victor ACC. 2004a. Seed production and juvenile rearing of the tropical abalone *Haliotis varia* Linnaeus 1758. *Aquaculture* 234:277–92.
- Najmudeen TM, Victor ACC. 2004b. Reproductive biology of the tropical abalone *Haliotis varia* from Gulf of Mannar. *Journal of the Marine Biological Association of India* 46:154–61.
- Oates MD, Cooper BR, Jorgenson JW. 1990. Quantitative amino acid analysis of individual snail neurons by open tubular liquid chromatography. *Analytical Chemistry* 62:1573–7.
- Pazos AJ, Roman G, Acosta CP, Sanchez JL, Abad M. 1997. Lipid classes and fatty acid composition in the female gonad of *Pecten maximus* in relation to reproductive cycle and environmental variables. *Comparative Biochemistry and Physiology* 117:393–402.
- Sastry AN, Blake NJ. 1971. Regulation of gonad development in the bay scallop, *Aequipecten irradians* (Lamarck). *Biological Bulletin of the Marine Biology Laboratory, Woods Hole* 140:274–83.
- Snedecor GW, Cochran WG. 1967. *Statistical Methods*. New Delhi: Oxford and IBH Publishing.
- Soudant P, Marty Y, Moal J, Robert R, Quere C, Le Coz JR, Samain JF. 1996. Effect of food fatty acid and sterol quality on *Pecten maximus* gonad composition and reproduction process. *Aquaculture* 143:361–78.
- Tanaka S, Hatano H. 1952. Studies on the seasonal changes in the chemical constituents of the pearl oyster. *Seto Marine Biology Laboratory Publication* 2:341–55.
- Webber HH. 1967. Changes in metabolite composition during the reproductive cycle of the abalone *Haliotis cracherodii* (Gastropoda: Prosobranchiata). *Physiological Zoology* 43:213.
- Webber HH, Giese AC. 1969. Reproductive cycle and gametogenesis in the black abalone, *Haliotis cracherodii* (Gastropoda: Prosobranchiata). *Marine Biology* 4:152–9.
- Wood AD, Buxton CD. 1996. Aspects of the biology of the abalone *Haliotis midae* (Linne, 1959) on the east coast of South Africa. 2. Reproduction. *South African Journal of Marine Sciences* 17:69–78.

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