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Aspects of reproduction of the brown mussel *Perna perna* at the Iture rocky beach near Cape Coast, Ghana

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Aspects of the reproductive biology of the brown mussel *Perna perna* at the Iture rocky beach near Cape Coast, Ghana, were studied from September 2014 to August 2015. The current study was aimed at providing information useful for managing the mussel fishery in this locality and also that would form the basis for designing appropriate culture methods for the species. Microscopic examination of fresh smears of gonadal material, as well as histological preparations of the gonad, were used to study the sexuality and breeding pattern of the species. Monthly gonadal and condition indices were also determined. *Perna perna* exhibited gonochoristic sexuality with a sex ratio of approximately 1:1 throughout the study period. Sexes were identifiable at shell lengths of 15.0–19.9 mm. Five stages of gonadal development were identified in both sexes. Gametogenic activity was continuous throughout the year, with two major spawning activities, from April to June and from August to December. These periods coincided with the major and minor rainy seasons, respectively, as well as the major upwelling period in August. Condition indices suggest that the mussels were in better condition for harvesting in March and August prior to the major spawning events.

Keywords: condition index, gonad, histology, sexuality, spawning

Introduction

The genus Perna belongs to the Mytilidae, the family of 'true mussels', which includes green- and brownshelled mussels from tropical, subtropical, warm- and cold-temperate regions (Gosling 2003). According to Siddall (1980) and Shafee (1989), there are only three extant species in this genus, each having a specific geographical distribution: (i) P. viridis occurs in Asian waters, but has been introduced into North and South America, Australia (Gobin et al. 2013) and South Africa (Micklem et al. 2016 and references therein); (ii) P. canaliculus occurs in New Zealand coastal waters; and (iii) P. perna occurs on the African coast and the east coast of South America. They are described by Harley (2011) as dominant species on rocky shores, often forming continuous beds in the intertidal and shallow subtidal regions and providing microhabitats for many species. According to Shafee (1989), warm-water mussels belonging to the genus have attracted considerable research interest because of their economic importance and they are farmed extensively on a commercial scale in several countries (Sreedevi et al. 2014).

Common along the West African coast, the brown mussel *Perna perna* (Linnaeus, 1758) is attached by bysus threads to rocks from the mid- to lower shore, especially on exposed coasts (Yankson and Kendell 2001). It is among popular bivalves in Ghana collected from the wild for consumption. Apart from being a cheap source of protein for coastal communities, *P. perna* is also considered one of the bivalves with high potential for culturing in Ghana (Yankson 2004). Recent intense trading in this species has

resulted in heavy exploitation, particularly in municipalities such as the Cape Coast Metropolitan and Elmina in the Central Region of Ghana.

Knowledge of the reproductive cycle of a species is important for fisheries management (da Costa et al. 2012). Information on gamete release in bivalves is essential, because the release has been reported to have an immediate and important effect on the market value of the adult stock, given that more than half the total wet mass of flesh can be lost in a single spawning event (van Erkom Schurink and Griffiths 1991). Hence the information is useful in predicting when mussels are in suitable condition for harvesting. The most reliable methods for studying the reproductive cycle in bivalves are those based on either histological or squash preparations of the gonads (Gosling 2003), where observations are made at regular intervals throughout the year to identify the progressive development of oocytes and the subsequent changes in morphology of the gonad tissue over time (Seed 1976; Seed and Suchanek 1992).

Generally, information on the biology of *P. perna* on the west coast of Africa is scant, but the population and reproductive dynamics of the species have been well described in South Africa (Berry 1978; Crawford and Bower 1983; Lasiak 1986; Lasiak and Dye 1989; van Erkom Schurink and Griffiths 1991; Lasiak and Barnard 1995; Tomalin 1995; Zardi et al. 2007), northern Africa (Abada-Boudjema et al. 1984; Shafee 1989, 1992; Abada-Boudjema and Dauvin 1995), India and Sri Lanka (Appukuttan et al. 1989; Indrasena and Wanninayake 1994), Brazil (Lunetta 1969), Venezuela (Carvajal 1969; Vélez and Epifanio 1981; Bigatti et al. 2005) and Texas (Hicks et al. 2001). In Ghana, *P. perna* has been reported regarding only its distribution and composition in relation to other macroinvertebrates (Yankson and Akpabey 2001; Intsiful 2002) and heavy metal content (Otchere 2003). The current study aimed to evaluate the sex ratio, size at onset of sexual maturity, reproductive cycle and the spawning pattern of *P. perna* at the Iture rocky beach.

Material and methods

Study area

The study was carried out at the Iture rocky beach near Cape Coast in the Central Region of Ghana. The location of the Iture rocky beach, as described by Yankson and Akpabey (2001), is approximately 6 km west of Cape Coast and 3 km east of Elmina (5°05′0.14″ N, 1°10′19.9″ W) (Figure 1). It is a relatively narrow beach measuring up to 60 m from the mean low water mark to the uppermost limit. The general slope of the beach is gentle (approximately 9°) and it conforms to the description of a moderately sheltered beach (Lawson 1956).

Measurement of hydrographic parameters

Several hydrographic parameters were measured monthly at low tide at the sampling site. Temperature, dissolved oxygen and pH of seawater were measured using a multipurpose water quality checker (Oakton PCD 650) and salinity was measured using a handheld refractometer. For each parameter three measurements were taken and the mean calculated.

Determination of sex and maturation stage

Sex and maturation stage of *P. perna* were determined by microscopic examination of fresh smears of gonadal material as well as histological preparations of the gonad during each month of the year, thus including the peak dry (February–March) and wet seasons (June–July). Mussels covering the entire size range of the population were randomly collected using four 0.25 m² quadrats. Small individuals that could not be sexed from smears of gonadal material were processed for histological analysis.

Examination of gonad development and analysis of breeding pattern

For monthly histological examination of gonad development, approximately 30 adult individuals were used, ranging in shell length from 30 to 75 mm. Parts of the visceral mass and mantle were fixed in Bouin's solution for 24 hours, washed and preserved in 70% alcohol and later subjected to standard histological methods prior to sectioning (Ampofo-Yeboah et al. 2009). Six 'serial' sections from three different portions of the gonad were cut at a thickness of 7–10 μ m, mounted on a microscope slide, stained with Ehrlich's haematoxylin, then counterstained with eosin. Prepared sections were examined microscopically to identify sex and gonad developmental stage following a five-stage scheme of gametogenic activity. The proportion of individuals in each developmental stage was

computed to assess the progression of gonad development and hence the breeding pattern. The monthly sex ratio of the adult population was determined from the histological analysis.

Gonad indices (GI) were calculated using a modified version of the 'index of gonad maturity' scheme proposed by Chipperfield (1953). Stages I (developing), II (ripening), III (ripe), IV (spawning) and V (resorption/redevelopment) were scored 1, 2, 3, 2 and 1, respectively. A mean GI for each month was calculated from the individual scores for gonad condition (Ndzipa 2002), according to the equation:

Mean GI =
$$\Sigma gn / N$$

where g is the score of the stage, n is the number of individuals assigned to the specific stage and N is the sample size.

The condition indices (CI) of the 30 mussels used for the histological preparation were determined monthly, prior to fixation. The displacement method adopted by Yankson (1986) was used, where CI was calculated as:

$$CI = \frac{Meat volume}{Whole volume - shell volume} \times 100$$

where meat, whole and shell volumes were the displacements (ml) caused by the meat (wiped dry with blotting paper), the intact mussel with the valves closed and the empty shell valves, respectively.

Statistical analysis

A Chi-square (χ^2) analysis was used to assess any deviations from an expected sex ratio of 1:1 for the mussels in each size class and also in the monthly adult samples.

Results

Hydrographic parameters

A summary of monthly hydrographic parameters of seawater at the study site for the period September 2014 to August 2015 is presented in Table 1. Temperature ranged between 26.5 and 31.8 °C, with the highest temperature recorded in March and the lowest in August. Dissolved oxygen (DO) concentration was relatively stable, ranging from 6.4 mg I⁻¹ in December to 7.5 mg I⁻¹ in August. Salinity fluctuated between 31 in June and 38 in February and pH varied from 5.8 in January to 8.2 in June.

Maturation and overall sex ratio

Figure 2 presents percentages of sexually undifferentiated, male and female mussels by size group. The data were pooled across the dry and wet seasons, because initial examination indicated similar results. The minimum size at sexual maturity, corresponding to the smallest individuals with mature gonads, was in the size class 15.0-19.9 mm. All individuals <15 mm in shell length did not have identifiable gonads. No hermaphrodite was found in any of the size groups. Sex ratio did not deviate significantly from 1:1 (p > 0.05) in all the mature size groups (Table 2), suggesting that the mussels were gonochoric



Figure 1: Map of Ghana, showing the Central Region and the Iture rocky beach

Table 1: Summary of mean values (SD) of hydrographic parameters at the iture rocky beach, September 2014–August	ugust 201
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Data	Hydrographic parameter						
Date	Temperature (°C)	Dissolved oxygen (mg l ⁻¹)	Salinity	рН			
14 September	27.3 (0.40)	7.4 (0.20)	35.3 (0.25)	7.5 (0.15)			
14 October	27.6 (0.05)	7.3 (0.05)	35.8 (0.25)	7.3 (0.10)			
14 November	30.3 (0.85)	6.7 (0.65)	34.1 (1.00)	6.6 (0.25)			
14 December	29.8 (0.10)	6.4 (0.50)	37.0 (1.00)	6.9 (0.19)			
15 January	29.5 (0.45)	7.3 (0.23)	37.7 (0.21)	5.8 (0.07)			
15 February	30.6 (0.65)	6.7 (0.65)	38.0 (0.50)	6.2 (0.19)			
15 March	31.8 (0.20)	6.6 (0.28)	33.0 (1.18)	7.8 (0.48)			
15 April	30.2 (0.65)	6.7 (0.12)	30.0 (1.15)	6.5 (0.21)			
15 May	29.9 (0.70)	7.0 (0.28)	32.5 (1.50)	6.6 (0.08)			
15 June	27.6 (0.10)	6.9 (0.41)	31.0 (1.00)	8.2 (0.04)			
15 July	27.0 (0.15)	7.1 (0.21)	34.1 (1.86)	7.9 (0.14)			
15 August	26.5 (0.21)	7.5 (0.05)	37.5 (0.71)	6.7 (0.32)			

(i.e. dioecious). Of the 583 mussels examined, 261 (44.77%) were males, 258 (44.26%) were females and 64 (10.97%) were undifferentiated.

Gonad development, monthly adult sex ratio and breeding pattern

The stages of gametogenic activity identified in the gonadal histology of mature individuals from the Iture rocky beach,

following the scheme of Ampofo-Yeboah et al. (2009), are illustrated in Figure 3.

Stage I: developing

Mussels in this stage had small follicles within the gonadal connective tissue. Cells within follicles were mostly primary oocytes in females (Figure 3: 1a) and spermatocytes in males (Figure 3: 1b).



Figure 2: Sexual differentiation in Perna perna from the Iture rocky beach. Labels represent sample size

Table 2: Sex ratio of Perna perna by size group from the Iture rocky beach, September 2014-August 2015

Size group (mm)	Undifferentiated	Male	Female	Total	Sex ratio (M:F)	χ ²	р
5.0-9.9	30	0	0	30	_	_	_
10.0–14.9	13	0	0	13	-	_	_
15.0–19.9	5	6	4	15	1:0.7	0.400	ns
20.0-24.9	2	9	10	21	1:1.1	0.053	ns
25.0-29.9	9	21	23	53	1:1.1	0.091	ns
30.0-34.9	5	42	40	87	1:0.9	0.049	ns
35.0-39.9	0	65	57	122	1:0.9	0.525	ns
40.0-44.9	0	48	65	113	1:1.4	2.558	ns
45.0-49.9	0	35	33	68	1:0.9	0.059	ns
50.0-54.9	0	22	17	39	1:0.8	0.641	ns
55.0-59.9	0	6	4	10	1:0.7	0.400	ns
60.0-64.9	0	7	5	12	1:0.7	0.333	ns
Total	64	261	258	583	1:1.0	0.017	ns

ns = not significant ($\alpha = 0.05$)

Stage II: ripening

In this stage, follicles were expanding, displacing most gonadal connective tissues. Follicles contained predominantly oocytes in females (Figure 3: 2a) and spermatocytes and some spermatozoa in males (Figure 3: 2b).

Stage III: ripe

Mussels in this stage had gonads entirely filled with expanded follicles. Follicles contained matured ova (Figure 3: 3a) in females and spermatozoa (Figure 3: 3b) in males.

Stage IV: spawning

Mussels in this stage had recently released or were in the process of releasing gametes, as indicated by expanded follicles containing spaces formerly occupied by matured gametes (Figure 3: 4a, 4b). In males, the spermatozoa were less compact compared to the ripe stage. Follicle walls were thin and broken.

Stage V: resorption/redevelopment

This stage was characterised by shrunken follicles with a few residual gametes undergoing resorption and redevelopment (production of primary oocytes and spermatocytes was visible) (Figure 3: 5a, 5b).

Of the total of 325 adults sampled for histological analysis, 161 (49.54%) were males, 149 (45.83%) were females and the sexes of 15 (4.62%) were indeterminate. The predominance of males was not significant ($\chi^2 = 0.465$, p > 0.05) at a sex ratio of 1:0.93 (male:female). Monthly sex ratio also did not show seasonal variation



Figure 3: Photomicrographs of gametogenic stages of *Perna perna*: developing – (1a) female, (1b) male; ripening – (2a) female, (2b) male; ripe – (3a) female, (3b) male; spawning – (4a) female, (4b) male; resorption/redevelopment – (5a) female, (5b) male (magnification = ×300)

Month	п	Male	Female	Sex ratio	χ ²	р
September	28	17	11	1:0.65	1.286	ns
October	25	12	13	1:1.08	0.040	ns
November	20	12	8	1:0.67	0.160	ns
December	28	16	12	1:0.75	0.571	ns
January	21	13	9	1:0.69	0.809	ns
February	22	12	10	1:0.83	0.182	ns
March	26	13	13	1:1.00	0.000	ns
April	30	17	13	1:0.76	0.533	ns
May	29	14	15	1:1.07	0.034	ns
June	23	10	13	1:0.77	0.391	ns
July	28	12	16	1:1.3	0.571	ns
August	29	13	16	1:1.23	0.310	ns
Total	310	161	149	1:0.93	0.465	ns

Table 3: Monthly sex ratio of mature Perna perna from the Iture rocky beach, September 2014–August 2015

ns = not significant ($\alpha = 0.05$)



Figure 4: Proportions of Perna perna, from the Iture rocky beach, in the various gametogenic stages, September 2014-August 2015

from the theoretical 1:1 (p > 0.05) (Table 3). An analysis of the gametogenic cycle is represented in Figure 4 as the percentage distribution of the different reproductive stages. Gonad development in P. perna followed an annual cycle, with two major spawning events between April and June and between August and December. When sampling began in September 2014 mussels had already spawned or were in the process of spawning, as indicated by a high proportion (46.4%) of individuals in the resorption stage and 32.1% in the spawning stage. Spawning continued through to December. Gonad redevelopment began in October, with the developing stage becoming increasingly dominant until approximately February. Mussels with ripening (late development) gonads dominated (55.2%) in March, before spawning occurred again from April to June. The rapid development of follicles occurred in July before the second major spawning event began in August.

Gonad indices, calculated from the staging of the gonads of individual mussels, indicated that gametogenic activity occurred to a varying extent throughout the year (Figure 5). The lowest value of 1.1 was recorded in January 2015, whereas the highest value of 2.0 was recorded in March 2015. Increasing values between consecutive sampling periods were indicative of gonadal growth and development, whereas decreasing values suggested spawning or resorption of gametes.

The condition index of sexually mature *P. perna* fluctuated monthly (Figure 5). The index values increased with gonad development and the highest value coincided with a high proportion of ripening individuals in the population. However, the values declined with spawning.

The various hydrographic parameters measured did not have any direct relationship with gonad development (as measured by GI) or with CI, as depicted by the correlation coefficients in Table 4.



Figure 5: Monthly variations in gonad and condition indices of Perna perna from the Iture rocky beach, September 2014-August 2015

Table 4: Pearson's correlation coefficient between measured hydrographic parameters and condition and gonad indices of *Perna perna* at the lture rocky beach

	Temperature	Dissolved oxygen	Salinity	рН
Condition index	0.344	-0.183	0.298	-0.195
<i>p</i> -value	0.274	0.568	0.348	0.543
Gonad index	0.025	0.003	-0.542	0.345
<i>p</i> -value	0.938	0.992	0.068	0.302

Discussion

The current study has shown that *P. perna* at the Iture rocky beach becomes sexually mature at between 15.0 and 19.9 mm shell length. According to Gosling (2003), the age (length) at which bivalves become sexually mature differs among species. For example, sexual maturation in *P. viridis* from Asia begins at a length of 15–30 mm (Sidall 1980; Vakily 1989) and Bigatti et al. (2005) observed that sexual differentiation in *P. viridis* in Venezuela began at a length of 20 mm and that no gonadal development was observed in individuals <18 mm in length.

Whereas functional ambisexuality has been reported as a common feature among molluscs, such as the Pisiididae, Tridacnidae, Pectinidae and Anomalodesmata (Lee 1988), most studies on the Mytilidae suggest stable gonochorism, with only occasional hermaphroditism, e.g. *Mytilus edulis* (Seed 1976; Lee 1988), *Choromytilus meridionalis* and *Aulacomya ater* (Griffiths 1977; Lee 1988). The current study indicated that males and females were equally distributed in all size groups, which was corroborated by a monthly sex ratio of 1:1 within adults. No hermaphrodites were encountered, indicating that *P. perna* at the Iture rocky shore is gonochoric (dioecious). This concurs with earlier reports that the sexes in *Perna* spp. are generally separate (Yap et al. 1979; Walter 1982; Vakily 1989) and that the occasionally reported occurrence of hermaphrodites might have resulted from misidentification (Lee 1988).

In marine bivalves the reproductive cycle can occur annually, semi-annually or continuously, depending on the species and environmental conditions (Sastry 1979; Newell et al. 1982). In the current study, gonad development in *P. perna* was continuous through the year, with peak activity in March and again in July. The first major spawning event occurred in the wet season (April-June) and the second major spawning event took place over an extended period (August-December), which coincided with relatively low water temperature and high salinity conditions resulting from upwelling of colder, nutrient-rich water masses (Ofori-Adu 1975, 1978; Mensah and Koranteng 1988). An extended/continuous annual cycle of gametogenesis, with two or more spawning events, has been reported before for the genus Perna in the more stable environmental conditions that prevail in the tropics (Parulekar et al. 1982; Walter 1982; Tuaycharoen et al. 1988; Vakily 1989). For example, Sokołowski et al. (2010) reported two major spawning events for P. perna from the coastal waters of Yemen, as did Zardi et al. (2007) for P. perna (and Mytilus galloprovincialis) on the south coast of South Africa, although that is a temperate region. However, off the Venezuelan coast, larval surveys indicated three spawning periods for P. perna (Carvajal 1969).

In addition to the use of histology, gonad indices have been used widely to determine spawning periodicity in bivalves, with the combined techniques resulting in increased confidence in the determination of spawning periodicity. In the current study, GI values at or just below 2.0, which indicate periods of maximal gonad development (Barber et al. 2005), occurred in March and August. These two peaks suggest two major spawning events in *P. perna*, which is consistent both with observations of monthly variations in CI and in the gonad histological analysis.

The CI of bivalves is used to describe the degree of fatness or the extent to which the meat fills the shell (Quayle 1980), which is useful information for bivalve farmers as it indicates the commercial quality of the animals (Davenport and Chen 1987). Monitoring the index in mussels is therefore necessary to determine the most suitable time(s) of the year for harvesting (Yankson 2004). Seasonal changes in CI result from complex interactions of a variety of factors, including food, temperature and salinity and the metabolic activities of mussels. particularly the growth and reproductive processes (Hickman and Illingworth 1980; Thippeswamy and Joseph 1988). Seasonal variations in CI of Perna have been reported for P. viridis (Vakily et al. 1988; Hemachandra and Thippeswamy 2008), P. canaliculus (Marsden and Weatherhead 1999) and P. perna (Galvao et al. 2015). Hemachandra and Thippeswamy (2008) found that in most bivalves gonadal growth before spawning results in an increase in the total bulk as the gonad forms the major part of the visceral mass. In the current study, mean CI, reflecting the average meat condition of the mature mussels, fluctuated in a pattern similar to that of gonadal development activity, which peaked in March and July. The mean CI of P. perna was relatively high in March and August, which corresponded with maximum gonad developmental activity. The relatively low values recorded in January and in June corresponded with resorption/ redevelopment and the spawning period, respectively, in the mussels under study, which concurs with Hemachandra and Thippeswamy (2008).

In the current study, no direct relationship was identifiable between the individual hydrographic parameters measured and either gonad development or condition index. It is possible, however, that these environmental parameters might have an interactive effect, although our analysis did not consider potential interactions.

In summary, sex of the *P. perna* population at Iture was identifiable at a shell length of 15.0–19.9 mm. The overall sex ratio was 1:1. This sex ratio was found among all the size groups, indicating a gonochoristic sexuality. Gametogenic activity occurred continuously throughout the year, with two spawning peaks, the first occurring from April to June and coinciding with the major rainy season and the second from August to December, coinciding with the upwelling period and the minor rainy season. Monthly GI analysis revealed a high proportion of sexually ripe individuals in March and August. Consequently, individuals with ripe gametes can be collected during these months for maximum hatchery production of seed for commercial aquaculture. In addition, mature individuals are in better condition for harvesting at approximately the same period.

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References

- Abada-Boudjema Y[-M], Altes J, Moueza M. 1984. Croissance comparée de deux espéces de moules *Mytilus galloprovincialis* (Lmk.) et *Perna perna* (L.) dans une moulié naturelle de la baie d'Alger. *Haliotis* 14: 33–38.
- Abada-Boudjema Y-M, Dauvin J-C. 1995. Recruitment and lifespan of two national mussel populations *Perna perna* (Linnaeus) and *Mytilus galloprovincialis* (Lamarck) from the Algerian Coast. *Journal of Molluscan Studies* 61: 467–481.
- Ampofo-Yeboah A, Owusu-Frimpong M, Yankson K. 2009. Gonad development in the freshwater oyster, *Etheria elliptica* (Bivalvia: Etheriidae) in northern Ghana. *African Journal of Aquatic Science* 34: 195–200.
- Appukuttan KK, Nair TP, Thomas KT. 1989. Spat settlement of brown mussel *Perna indica* Kuriakose and Nair in the southwest coast of India. *Journal of Marine Biology Association of India* 31: 266–275.
- Barber BJ, Fajans JS, Baker SM, Baker P. 2005. Gametogenesis in the non-native green mussel, *Perna viridis*, and the native scorched mussel, *Brachidontes exustus*, in Tampa Bay, Florida. *Journal of Shellfish Research* 24: 1087–1095.
- Berry PF. 1978. Reproduction, growth and production in the mussel, *Perna perna* (Linnaeus), on the east coast of South Africa. *Investigational Report* No. 48. Durban: Oceanographic Research Institute.
- Bigatti G, Miloslavich P, Penchaszadeh PE. 2005. Sexual differentiation and size at maturity of invasive mussel *Perna viridis* (Linnaeus, 1758) (Mollusca: Mytilidae) at La Restinga Lagoon (Margarita Island, Venezuela). *American Malacological Bulletin* 20: 65–70.
- Carvajal JR. 1969. Fluctuación mensual de las larvas y crecimiento del mejillón *Perna perna* (L) y las condiciones ambientales de la Ensenada de Guatapanare, Estado Sucre, Venezuela. *Boletín del Instituto Oceanográfico de Venezuela* 8: 13–20.
- Chipperfield PNJ. 1953. Observations on the breeding and settlement of *Mytilus edulis* (L.) in British waters. *Journal of Marine Biology Association of the United Kingdom* 32: 449–476.
- Crawford RJM, Bower DF. 1983. Aspects of growth, recruitment and conservation of the brown mussel *Perna perna* along the Tsitsikamma coast. *Koedoe* 26: 123–133.
- da Costa FG, Aranda-Burgos JA, Cerviño-Otero A, Fernández-Pardo V, Louzán A, Nóvoa S et al. 2012. Clam reproduction. In: da Costa FG (ed.), *Clam fisheries and aquaculture*. New York: Nova Science. pp 45–71.
- Davenport J, Chen X. 1987. A comparison of methods for the assessment of condition in the mussel (*Mytilus edulis* L.). *Journal* of *Molluscan Studies* 53: 293–297.
- Galvao P, Longo R, Paulo J, Torres JPM, Malm O. 2015. Estimating the potential production of the brown mussel *Perna perna* (Linnaeus, 1758) reared in three tropical bays by different methods of condition indices. *Journal of Marine Biology* 2015: Article ID 948053 (11 pp).
- Gobin J, Agard J, Madera J, Mohammed A. 2013. The Asian green mussel *Perna viridis* (Linnaeus 1758): 20 years after its introduction in Trinidad and Tobago. *Open Journal of Marine Science* 3: 62–65.
- Gosling E. 2003. *Bivalve molluscs biology, ecology and culture*. Oxford: Blackwell Publishing Ltd.
- Griffiths RJ. 1977. Reproductive cycles in littoral populations of Choromytilus meridionalis (Kr.) and Aulacomya ater (Molina) with

a quantitative assessment of gamete production in the former. Journal of Experimental Marine Biology and Ecology 30: 53–71.

- Harley C. 2011. Climate change, keystone predation, and biodiversity loss. Science 334: 1124–1127.
- Hemachandra, Thippeswamy S. 2008. Allometry and condition index in green mussel *Perna viridis* (L.) from St Mary's Island off Malpe, near Udupi, India. *Aquaculture Research* 39: 1747–1758.
- Hickman RW, Illingworth J. 1980. Condition cycle of the greenlipped mussel *Perna canaliculus* in New Zealand. *Marine Biology* 60: 27–38.
- Hicks DW, Tunnell JW, McMahon RF. 2001. Population dynamics of the nonindigenous brown mussel *Perna perna* in the Gulf of Mexico compared to other world-wide populations. *Marine Ecology Progress Series* 211: 181–192.
- Indrasena WM, Wanninayake TB. 1994. Introduction of the marine brown mussel, *Perna perna*, into a brackish water lagoon for commercial raft culture. *Bulletin of Aquaculture Association of Canada* 94: 33–35.
- Intsiful G. 2002. Observation on the ecology of some edible macroinvertebrates on rocky beaches of Ghana and the levels of their exploitation. MPhil thesis, University of Cape Coast, Ghana.
- Lasiak T[A]. 1986. The reproductive cycles of the intertidal bivalves *Crassostrea cucullata* (Born, 1778) and *Perna perna* (Linnaeus, 1758) from the Transkei Coast, southern Africa. *The Veliger* 29: 226–230.
- Lasiak TA, Barnard TCE. 1995. Recruitment of the brown mussel *Perna perna* onto natural substrata: a refutation of the primary/ secondary settlement hypothesis. *Marine Ecology Progress Series* 120: 147–153.
- Lasiak T[A], Dye A[H]. 1989. The ecology of the brown mussel Perna perna in Transkei, southern Africa: implications for the management of a traditional food resource. *Biological Conservation* 47: 245–257.
- Lawson GW. 1956. Rocky shore zonation on the Gold Coast. The Journal of Ecology 44: 153–170.
- Lee SY. 1988. The reproductive cycle and sexuality of the green mussel *Perna viridis* (L.) (Bivalvia: Mytilacea) in Victoria Harbour, Hong Kong. *Journal of Molluscan Studies* 54: 317–323.
- Lunetta JE. 1969. Reproductive physiology of the mussel *Mytilus* perna. Boletim da Faculdade de Filosofia Ciências e Letras da Universidade de São Paulo, Serie Zoologia 26: 33–111.
- Marsden ID, Weatherhead MA. 1999. Shore-level induced variations in condition and feeding of the mussel *Perna canaliculus* from the east coast of the South Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 33: 611–622.
- Mensah MA, Koranteng KA. 1988. A review of the oceanography and fisheries resources in the coastal waters of Ghana, 1981–1986. *Marine Fisheries Research Report* No. 8. Tema, Ghana: Research & Utilization Branch, Fisheries Department.
- Micklem JM, Griffiths CL, Ntuli N, Mwale M. 2016. The invasive Asian green mussel *Perna viridis* in South Africa: all that is green is not viridis. *African Journal of Marine Science* 38: 207–215.
- Ndzipa V. 2002. Synchronisation of breeding in populations of the brown mussel *Perna perna* on the south coast of South Africa. MSc thesis, Rhodes University, South Africa.
- Newell RC, Field JG, Griffiths CL. 1982. Energy balance and significance of microorganisms in a kelp bed community. *Marine Ecology Progress Series* 8: 103–113.
- Ofori-Adu DW. 1975. Beach hydrography and the inshore fishery of Ghana for the period 1968–71. *Marine Fisheries Research Reports* No. 5. Tema, Ghana: Fisheries Research Unit.
- Ofori-Adu DW. 1978. The occurrence of thermoclines on the shelf of Ghana and the significance of thermocline depth variations to the surface schooling fishes. *Marine Fisheries Research Reports* No. 6. Tema, Ghana: Fisheries Research Unit.
- Otchere FA. 2003. Heavy metals concentrations and burden in the bivalves (Anadara (Senilia) senilis, Crassostrea tulipa and Perna

perna) from lagoons in Ghana: model to describe the mechanism of accumulation/excretion. *African Journal of Biotechnology* 2: 280–287.

- Parulekar AH, Dalal SG, Ansari ZA, Harkantra SN. 1982. Environmental physiology of raft-grown mussels in Goa, India. *Aquaculture* 29: 83–93.
- Quayle DB. 1980. *Tropical oysters: culture and methods*. IDRC TS17e. Ottawa: International Development Research Centre.
- Sastry AN. 1979. Pelecypoda (excluding Ostreidae). In: Giese AC, Pearse JS (eds), *Reproduction of marine invertebrates. Molluscs: pelecypods and lesser classes*. New York: Academic Press. pp 113–292.
- Seed R. 1976. Ecology. In: Bayne BL (ed.), *Marine mussels: their ecology and physiology*. Cambridge: Cambridge University Press. pp 13–66.
- Seed R, Suchanek TH. 1992. Population and community ecology of *Mytilus*. In: Gosling EG (ed.), *The mussel* Mytilus: ecology, physiology, genetics and culture. New York: Elsevier. pp 87–169.
- Shafee MS. 1989. Reproduction of *Perna picta* (Mollusca: Bivalvia) from the Atlantic coast of Morocco. *Marine Ecology Progress Series* 53: 235–245.
- Shafee MS. 1992. Production estimate of a mussel population Perna picta (Born) on the Atlantic coast of Morocco. Journal of Experimental Marine Biology and Ecology 163: 183–197.
- Siddall SE. 1980. A clarification of the genus *Perna* (Mytilidae). *Bulletin of Marine Science* 30: 858–870.
- Sokołowski A, Bawazir AS, Sokołowska E, Wołowicz M. 2010. Seasonal variation in the reproductive activity, physiological condition and biochemical components of the brown mussel *Perna perna* from the coastal waters of Yemen (Gulf of Aden). *Aquatic Living Resources* 23: 177–186.
- Sreedevi PR, Uthayakumar V, Jayakumar R, Ramasubramanian V. 2014. Influence of rearing water temperature on induced gonadal development and spawning behaviour of tropical green mussel, *Perna viridis. Asian Pacific Journal of Reproduction* 3: 204–209.
- Thippeswamy S, Joseph MM. 1988. Seasonal variability of condition index in the wedge clam, *Donax incarnates* (Gmelin). In: Joseph MM (ed.), *The proceedings, first Indian fisheries forum.* Mangalore: Asian Fisheries Society, Indian Branch. pp 147–150.
- Tomalin BJ. 1995. Growth and mortality rates of brown mussels *Perna perna* (Linnaeus) in KwaZulu-Natal: a comparison between sites and methods using non-parametric length-based analysis. *South African Journal of Marine Science* 16: 241–254.
- Tuaycharoen S, Vakily JM, Saclow A, McCoy EW. 1988. Growth and maturation of the green mussel (*Perna viridis*) in Thailand. In: McCoy EW, Chongpeepien T (eds), *Bivalve mollusc culture research in Thailand*. ICLARM Technical Reports 19. Bangkok: Department of Fisheries; Manila: International Center for Living Aquatic Resources Management; and Eschbom: Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ). pp 88–101.
- van Erkom Schurink C, Griffiths CL. 1991. A comparison of reproductive cycles and reproductive output in four southern African mussel species. *Marine Ecology Progress Series* 76: 123–134.
- Vakily JM. 1989. *Biology and culture of mussels of the genus Perna*. Manila: International Center for Living Aquatic Resources Management; and Eschborn: Deutsche Gesellschaft für Technische Zusarnmenarbeit (GTZ).
- Vakily JM, Tuaycharoen S, Nugranad J. 1988. Analysis of length and weight characteristics of green mussel, *Perna viridis*, from the Gulf of Thailand. *Asian Fisheries Science* 1: 165–174.
- Vélez A, Epifanio CE. 1981. Effects of temperature and ration on gametogenesis and growth in the tropical mussel *Perna perna* (L.). *Aquaculture* 22: 21–26.
- Walter C. 1982. Reproduction and growth in the tropical mussel Perna viridis (Bivalvia: Mytilidae), Kalikasan. Philippine Journal of Biology 1: 83–97.

- Yankson K. 1986. Reproductive cycles of *Cerastoderma glaucum* (Bruguiere) and *C. edule* (L.) with special reference to the effects of the 1981–82 severe winter. *Journal of Molluscan Studies* 52: 6–14.
- Yankson K. 2004. Fish from the shell: its potential in the quest for adequate protein in Ghana. An inaugural lecture delivered at the University of Cape Coast. Accra, Ghana: Media Graphics & Press.
- Yankson K, Akpabey FJ. 2001. A preliminary survey of the macroinvertebrate fauna at Iture rocky beach, Cape Coast, Ghana. *Journal of Natural Sciences* 1: 11–22.

Yankson K, Kendal M. 2001. A student's guide to the fauna of sea

shores of West Africa. Darwin Initiative Report 1, Ref. 162/7/451. Penicuik, UK.

- Yap WG, Young AL, Orano CEF, de Castro MT. 1979. Manual on mussel farming. *Aquaculture Extension Manual* No. 6. Iloilo, Philippines: Aquaculture Department, Southeast Asian Development Center.
- Zardi GI, McQuaid CD, Nicastro KR. 2007. Balancing survival and reproduction: seasonality of wave action, attachment strength and reproductive output in indigenous *Perna perna* and invasive *Mytilus galloprovincialis* mussels. *Marine Ecology Progress Series* 334: 155–163.