Aquat. Living Resour. 23, 177–186 (2010)

DOI: 10.1051/alr/2010016
www.alr-journal.org

Aquatic Living Resources

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)

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Received 24 April 2009; Accepted 8 March 2010

Abstract – Gametogenic cycle, gross biochemical composition, condition indices and soft tissue caloric value of the brown mussel *Perna perna* were investigated in the coastal waters of the Gulf of Aden over ten months, to delineate ecophysiological performance of the bivalve. The timing of reproductive activity and seasonal variations of physiological features appear to depend on interaction of environmental (exogenous) and internal (endogenous) factors. Two major spawning events occurred during seasonal monsoons i.e. in late summer (SW monsoon, August-September) and early spring (NW monsoon, February-March), although these differed considerably in relative intensity and the extent of the resulting changes in physiology and body weight. The summer breeding, which was correlated with low water temperature and abundant food, exerted little effect on biochemical constituents, indicating protracted and portioned spawning. Reserve stores (lipids, carbohydrates and proteins) accumulated gradually in the cooler inter-monsoon period of gametogenic quiescence, to provide energy for periods of natural nutritional stress when water temperature increased and primary production diminished. The second spawning in spring was accompanied by a substantial decrease in lipids, carbohydrates and condition indices of the mussels probably due to the release of nutrient-rich gametes in adaptive response to lower food availability in the environment. High reproductive effort presumably induced increased mortality of females, which were strongly outnumbered by males at a ratio of 1.8:1.0. Caloric value of this mussel falls within a range typical for mussel species in other subtropical areas, highlighting the importance of *Perna perna* as a local food resource and its potential suitability for aquaculture.

Key words: Ecological physiology / Gametogenesis / Biochemical composition / Condition / Reproduction / Mollusca / *Perna perna*

Résumé – Nous avons étudié le cycle gamétogénétique, la composition biochimique, les indices de condition et la valeur calorique des tissus mous de la moule, *Perna perna* (Mytilidae), de la zone côtière du golfe d'Aden et durant 10 mois, afin d'estimer le comportement écophysiologique de ce bivalve. La période d'activité reproductrice et les variations saisonnières des caractéristiques physiologiques semblent dépendre de l'intéraction des facteurs environnementaux (exogènes) et internes (endogènes). Deux périodes principales de ponte se déroulent durant les moussons saisonnières, en fin d'été (mousson de sud-ouest, en août-septembre) et au début du printemps (mousson de nord-ouest, en février-mars), bien que celles-ci soient très différentes en intensité relative et en conséquences sur les changements physiologiques et sur le poids des mollusques. La ponte estivale, qui est corrélée avec une faible température de l'eau et une nourriture abondante, exerce peu d'effet sur les constituants biochimiques, montrant une ponte prolongée et fractionnée. L'accumulation de réserves (lipides, glucides et protéines) est effectuées graduellement durant la période de l'intermousson lors de température plus faible et du repos gamétogénétique, permet de fournir de l'énergie durant les périodes de stress nutritionnel lorsque la température augmente et la production primaire diminue. La seconde période de ponte au printemps est accompagnée par une forte diminution des lipides, glucides et des indices de condition chez les moules, probablement due à l'émission de gamètes et correspond à une réponse adaptative à la faible disponibilité

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en nourriture. Cet effort reproductif important induit probablement une augmentation de la mortalité des femelles, le nombre de mâles est alors majoritaire au taux de 1,8 :1,0. La valeur calorique de ces moules correspond à celle typique des espèces de moules d'autres zones sub-tropicales, mettant en évidence l'importance de *Perna perna* en tant que ressource locale alimentaire et son adéquation potentielle à l'aquaculture.

1 Introduction

The brown mussel *Perna perna* commonly inhabits subtropical and tropical areas of the Indo-Pacific, Atlantic coasts of northwestern and southern Africa and South America (Berry 1978; Siddall 1980), and recently colonised much of the Texan coast of the Gulf of Mexico (Hicks and Tunnell Jr 1993). The bivalve often constitutes an important component of epifaunal communities on a variety of hard substrata in the intertidal and shallow subtidal zones, contributing significantly to benthic secondary production (Berry and Schleyer 1983) and energy fluxes between pelagic and benthic systems. A wide geographic distribution across a range of environmental conditions indicates a broad adaptive capacity and ecophysiological plasticity of these mussels, enabling them to grow and reproduce successfully under different ecological conditions, and to extend spatially into new habitats (Hicks et al. 2001). The biological attributes of *P. perna*, including a rapid growth rate that allows mussels to reach a size of 50–70 mm in 6–7 months (Chung and Acuna 1981; Bawazir 2000), relative resistance of eggs and larvae to environmental stress and ability of adults to acclimatise to variable hydrological situations (Berry 1978; Siddall 1979), make the species especially suitable for cultivation. Indeed, large-scale aquaculture of the brown mussel has increased on the Atlantic coasts of Brazil (Soares et al. 2008) and Venezuela (Poza-Boveda 1992), providing important cultural, social and economic benefits.

The coastal waters of Yemen, in the Hadramaut district, receive a large injection of nutrients from the monsoon upwelling that stimulates planktonic and benthic algal growth along the shore over several months each year. The productivity of the upwelling area of the north western Indian Ocean, often exceeding 1.0 mg C m^{-3} h^{-1} in the upper 50 m water layer, has been found to be equal in magnitude to that of the Peruvian area (Smith 1984). This highly productive region of the Gulf of Aden is inhabited by a variety of benthic invertebrates and fish, some of which are exploited extensively by fisheries (Wagenaar and D'Haese 2007), e.g. the rock lobster *Panulirus homarus*, the deep-sea lobster *Periulus semelli*, the cuttlefish *Sepia pharaonis,* the yellowfin tuna *Thynus albacares* and sardine *Sardina pilchardus*. The brown mussel *P. perna* occupies (sometimes in great numbers) rocky outcrops and gravely sediments, particularly in semi-sheltered and shallow-water khawrs (small bays) or inlets, which occur as breaks in the sandy shore. The morphology of the Yemeni coastline, its limited hydrodynamics and high productivity appear thus to provide a favourable environment for development of benthic faunal communities, and also make the coastal zone of the Gulf of Aden favourable for shellfish mariculture. Pilot farming of *P. perna* proved successful in the Ash-shehr area (Al Murjan Marine Resources Company), highlighting the suitability of the mussel for commercial cultivation. However, biological and ecological studies of these mussels in the coastal waters of Yemen have still lagged behind those made in other subtropical regions (Berry and Schleyer 1983; Tavares et al. 1998).

The present study was set up to investigate temporal changes in reproductive activity, biochemical constituents and physiological status of *P. perna* from the Hadramaut district (Yemen), aiming to delineate variations in its ecophysiological performance during monsoon and inter-monsoon periods. Correlations were examined between physiological measurements and local environmental factors recorded at the same time as the mussel sampling. Energetic value of the soft tissue was additionally determined and compared among different species of the genus *Perna* and across different subtropical regions worldwide to assess the relative potential of brown mussels as a local food source and for mariculture.

2 Materials and methods

2.1 Hydrological parameters

Basic hydrological parameters of surface coastal waters (temperature, salinity, dissolved oxygen, total suspended particulate matter (TPM), chlorophyll *a* (chl *a*) and particulate organic matter (POM)) were monitored simultaneously at the mollusc sampling site. Temperature, salinity and the concentration of dissolved oxygen were measured directly after sampling mussels in the field, using a WTW Universal Pocket Meter MultiLine P4. TPM, chl *a* and POM were determined at the laboratory according to standard methods recommended for marine waters (Kramer et al. 1994).

2.2 Mussels *Perna perna*

2.2.1 Sampling and storage

The brown mussels were collected by hand from gently sloping rocks and rocky platform exposed in the intertidal zone at the Ash-shehr (Hadramaut district) site on the west coast of the Gulf of Aden, Yemen (latitude 14°44′ N, longitude 49°35′ E; Fig. 1), at monthly intervals from July 1997 to April 1998. The sampling location was chosen, based upon previous surveys of local macrobenthic communities, to represent wild populations of mussels in a relatively unpolluted area (Szefer et al. 1997; Sokolowski et al. 2004). Up to two hours after sampling, live specimens of *P. perna* were transported in cool moist conditions to aerated concrete open-air ponds (3.0 × 2.0 × 0.5 m) where they were allowed to depurate the contents of their alimentary ducts for 24 h in Whatman GF/C-filtered surface seawater at temperature and salinity corresponding to the natural environmental conditions of the source site (Table 1). Only individuals of a restricted size range 50.1–60.0 mm, corresponding to the age of two years i.e. fully mature mussels (Bawazir 2000), were taken to reduce

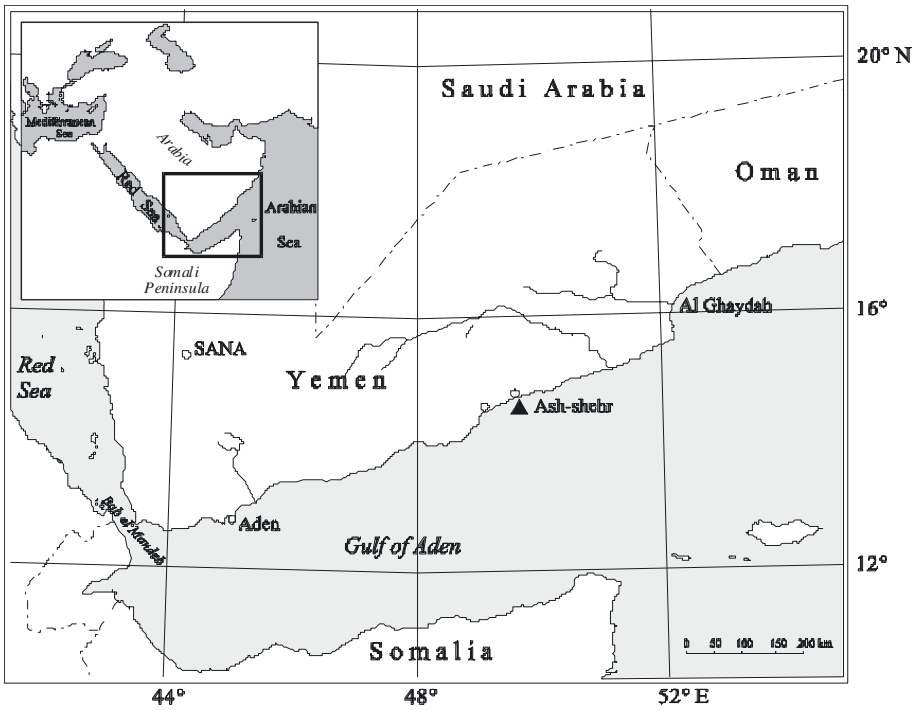

Fig. 1. Location of the sampling site on the coast of the Gulf of Aden (▲).

Table 1. Biometric data (mean ± SE) of *Perna perna* taken for biochemical analyses and reproductive cycle, with salinity and temperature of surface water in Ash-shehr on the coast of the Gulf of Aden, Yemen on up to 10 samplings between July 1997 and April 1998.

	Biochemical analyses		Reproductive cycle		Hydrological parameters	
Month	N^a	Shell length [mm]	N^b	Shell length [mm]	Temperature [°C]	Salinity
July	3(6)	54.9 ± 0.6	21	55.5 ± 0.6	24.4	36.6
Aug.	3(6)	54.7 ± 0.8	20	53.8 ± 0.9	26.0	36.2
Sep.	3(6)	54.6 ± 0.4	21	56.6 ± 0.7	25.7	36.7
Oct.	2(6)	59.8 ± 1.4	12	59.2 ± 1.0	26.7	36.8
Nov.	3(6)	55.9 ± 1.1	21	55.8 ± 1.8	25.6	35.2
Dec.	3(6)	55.7 ± 0.9	21	55.9 ± 1.4	25.2	35.2
Jan.	3(6)	51.3 ± 0.9	20	50.7 ± 0.9	25.4	35.2
Feb.	2(6)	51.8 ± 1.0	20	50.7 ± 1.7	25.5	35.6
March	2(6)	51.1 ± 0.8	20	52.3 ± 2.1	26.4	35.7
April	2(6)	51.5 ± 1.2	16	50.3 ± 0.9	28.0	35.8

[a]Number of pooled samples, with number of individuals per sample in parentheses.
[b]Number of individuals per sample.

potential size effects on the ecophysiological measurements on these bivalves (Fatima 1996). This fraction represented the most abundant size mode of the entire population. Shells were cleaned of epibionts (seaweeds and the associated fauna) and debris, and the byssus was discarded.

2.2.2 Body weight, condition indices (CI) and biochemical constituents

Individual shell length of 12–18 mussels was recorded to the nearest 0.01 mm using a digital calliper at each sampling. The bivalves were then deshelled and individual soft tissue wet weight (WW) was measured following water removal with tissue paper. After air-drying at 55 °C to a constant weight (36–48 h), soft tissue was weighed (ash dry weight, ADW) and homogenized in a commercial mortar. Two to three pools of six individuals each were kept frozen in polyethylene vials at –20 °C until the time of analysis (Table 1).

Two morphological indices were calculated for 12–18 mussels at each month: weight index (CI1), as the soft tissue weight after drying (mg) per length^3 (cm^3); and % solids (CI2) as the ratio of soft tissue dry weight × 100 (mg) to soft tissue wet weight (mg). These indices were also evaluated in a selection of other bivalves to avoid variation associated with wet weight (Hickman and Illingworth 1980; Lucas and Beninger 1985).

The protein content was measured according to the Folin-Ciocalteu method of Lowry et al. (1951). Lipids

were extracted following the chloroform-methanol method of Bligh and Dyer (1959) and measured as described by Marsch and Weinstein (1966). Total carbohydrate and glycogen contents were determined according to the phenol-sulphuric acid method (Dubois et al. 1956). Ash content was determined by combusting the powdered tissue at 450 °C for 12 h. In addition, the caloric value of dry soft tissue was measured on pooled samples (n = 3) from July to December i.e. during a period of high individual body weight with a MI 100 Philipson KMB-2 microbomb calorimeter. For the purpose of geographical comparison, energy value was also estimated from the biochemical components, using the standard conversion factors: 23.6 kJ g^{-1} for protein (Brody 1945), 36.0 kJ g^{-1} for lipid and 17.2 kJ g^{-1} for carbohydrate (Beukema and de Bruin 1979).

2.2.3 Gametogenic cycle

At each sampling, 12 to 21 randomly chosen individuals of shell length 51.1–60.0 mm (Table 1) were fixed in 4% formaldehyde solution for gonad development study. Reproductive status was determined by the appearance of the gonad and reproductive cells under the microscope. From these macro- and microscopic observations, the condition of the gonads was classified into five main categories, *viz.* immature, developing, ripe, spawning and spawning/resting, following the scheme adopted by Caddy (1967) and Keck et al. (1975). Gonad index (GI, calculated by multiplying the number of individuals at each development stage by the numerical ranking of that stage [immature = 1, developing = 2, ripe = 3, spawning = 4 and spawning/resting = 0], and dividing the result by the total number of individuals in the sample) was also computed, following Chipperfield (1953), and sex ratio was determined.

2.2.4 Statistical analysis

Due to non-normal distribution (Kolmogorov-Smirnov test for goodness of fit) and non-homogenous variances (Bartlett's test) in most data, and unequal sample size, a non-parametric approach was used in the statistical models. The functional relation between pairs of variables was described by Spearman's rank correlation analysis and mean data were compared with respect to month by Kruskal-Wallis tests at a significance level of p = 0.050. General estimates explaining variation in physiological and biochemical results in terms of environmental parameters were obtained by Multiple Regression Analysis. Statistical analyses were carried out using Statistica 8.1 software (Sokal and Rohlf 1995).

3 Results

3.1 Environmental variables

Hydrological parameters of the nearshore waters on the southwest coast of the Gulf of Aden over the study period were included in the analysis, following Sokołowski et al. (2004).

Table 2. Trophic conditions (mean ± SE) of surface coastal waters at Ash-shehr (the Hadramaut district) on the west coast of the Gulf of Aden, Yemen between July 1997 and April 1998.

Month	TPM[a] (mg dm^{-3})	Chl *a* (mg dm^{-3})	POM (mg dm^{-3})
July	19.44 ± 1.16	2.77 ± 0.14	2.8 ± 0.2
Aug.	42.34 ± 2.54	3.93 ± 0.09	4.7 ± 0.5
Sep.	16.50 ± 1.24	0.84 ± 0.04	2.2 ± 0.2
Oct.	14.49 ± 0.78	0.72 ± 0.03	1.0 ± 0.1
Nov.	18.02 ± 1.30	2.65 ± 0.13	4.0 ± 0.4
Dec.	39.60 ± 3.30	1.55 ± 0.09	4.0 ± 0.4
Jan.	36.08 ± 3.45	1.32 ± 0.08	3.5 ± 0.4
Feb.	41.98 ± 3.51	1.94 ± 0.11	5.5 ± 0.6
March	36.91 ± 2.83	1.32 ± 0.07	5.5 ± 0.6
April	26.26 ± 1.64	1.02 ± 0.04	2.6 ± 0.2

[a]TPM: Total particulate matter, Chlorophyll *a* concentration (Chl *a*), Particulate organic matter (POM),

Briefly, two main periods of divergent hydrographic characteristics can be distinguished over the year: summer-early autumn (July through September/October) and autumn-spring (November through March), corresponding to two seasonal monsoons. During the SW monsoon, strong offcoast winds induce tropical upwelling, which results in lowered water temperature, relatively high salinity and good oxygenation near the coast with a maximum in July. Nutrient enrichment of surface waters due to upwelling and gradually increasing temperature enhance phytoplanktonic production in the water column (Table 2). In autumn and winter months, water temperature and salinity decrease, reaching their minimal levels in December. This is accompanied by a marked rise in TPM and a simultaneous decline in the concentration of chlorophyll *a*, indicative of the beginning of the NE monsoon season. The NE monsoon brings short but torrential rains (USOCD 1982), which cool down and dilute the surface seawater and increase local input of terrestrial material to the coastal zone through a system of small and numerous wadies. In spring, despite mild meteorological conditions and rising water temperature, non-organic and phytoplanktonic seston decrease due to limited water dynamics and low nutrient concentration.

3.2 Soft tissue weights, physiological condition, biochemical composition and tissue energetics

Shell length of the mussels taken for biochemical analyses did not differ significantly among months (Kruskal-Wallis test); the size of bivalves collected for reproductive cycle study did not differ among samplings either (Kruskal-Wallis test). Individual soft tissue wet and dry weights of *P. perna* showed apparent seasonal variations (Kruskal-Wallis test, $p < 0.036$ for both tests) with similar temporal patterns (Spearman's rank correlation analysis, $p < 0.018$). Both tissue weights reached their maximum levels in mid-summer (July; 4.67 g WW and 0.89 g ADW), at the beginning of the SW monsoon, then fell gradually through late summer (September-October; Fig. 2a). There was a substantial recovery of weight attributable to energy reserve accumulation in late autumn and winter (October-December), followed by a sharp decrease to minimum values

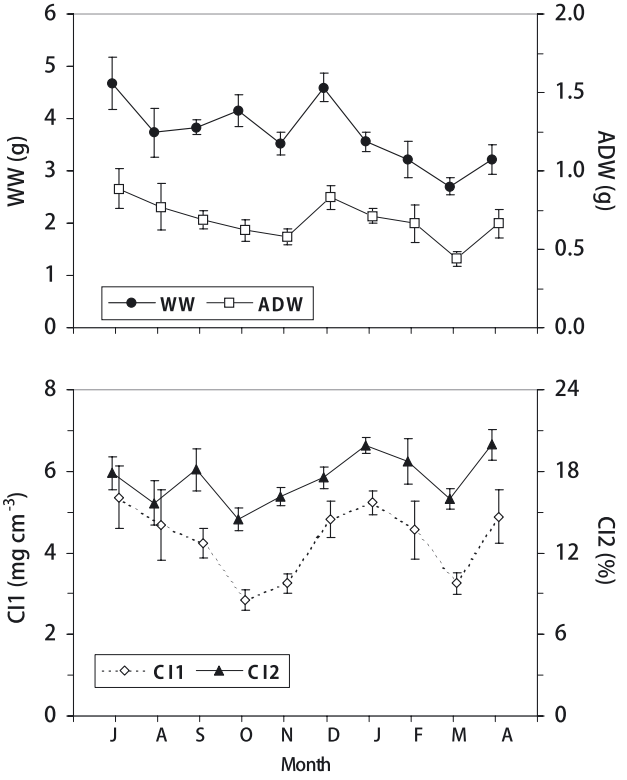

Fig. 2. Seasonal variations in soft tissue wet (WW) and ash dry (ADW) weights (a) and Condition indices: weight index (CI1) and % solids (CI2) as the ratio of soft tissue dry weight × 100 (mg) to soft tissue wet weight (mg) (b) of the brown mussel *Perna perna* in the coastal waters of the Gulf of Aden, Yemen. Data are presented as means ± SEM from two or three replicate samples.

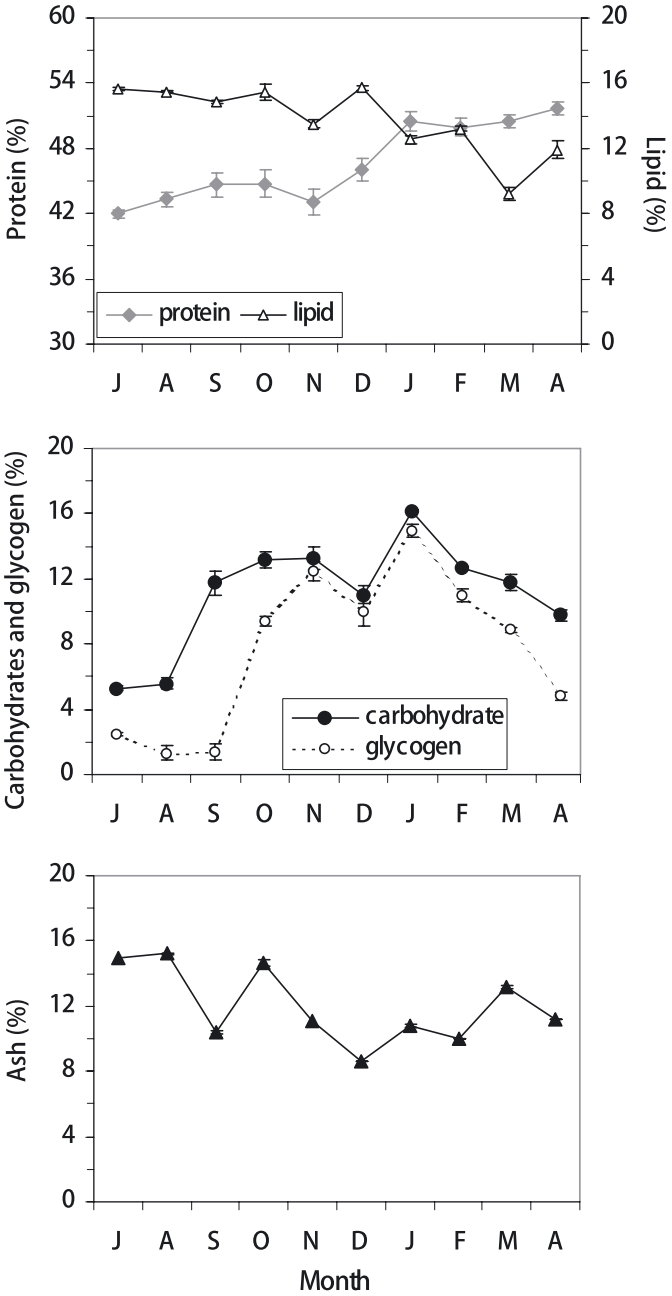

Fig. 3. Seasonal variations in the contents of biochemical constituents (protein, lipid, carbohydrates and glycogen) and ash of the brown mussel *Perna perna* in the coastal waters of the Gulf of Aden, Yemen. Data are presented as means ± SEM from two or three replicate samples.

in early spring (February-March, 2.70 g WW and 0.44 g ADW).

The condition indices (CI1, CI2), biochemical constituents (protein, lipid, carbohydrates/glycogen) and ash content of the soft tissue of *P. perna* demonstrated clear seasonal changes (Kruskal-Wallis test, $p < 0.011$ for all tests) over the study period. The two condition indices varied with season in a similar manner (Spearman's rank correlation analysis, $p < 0.050$), with elevated values in mid-summer (July) and winter (December-January), and generally reflected the temporal pattern of individual soft tissue dry weight (Fig. 2). After summer body weight gain in the late summer and autumn months, soft tissue weight and condition indices of the mussels decreased to a minimal level in October (2.8 mg cm^{-3} and 14.5% for CI1 and CI2, respectively), to increase again rapidly at the beginning of the NW monsoon. A spring decline in body weight brought about a decrease in the condition indices which reached almost the same low level as in autumn (3.3 mg cm^{-3} and 16.0% for CI1 and CI2, respectively).

A similar pattern of seasonal variations to that of soft tissue wet and dry weights was observed for lipid (Spearman's rank correlation analysis, $p < 0.029$ in both cases), which constituted from 9.2% to 15.7% of mussel dry weight. Lipid remained fairly high through summer and winter (13.5%–15.6%) with a maximum value in December (15.7%; Fig. 3); it then fell sharply to a minimum in March (9.2%). Surprisingly, high summer lipid reserves coincided with a decline in carbohydrates down to 5.3% and a decline in glycogen down as low as 11.8%. Carbohydrate accumulated steadily in autumn, decreased slightly in December and then increased further during the winter months up to 16.1% and 14.9% in January for carbohydrate and glycogen, respectively. The second but less marked reduction in carbohydrate content (down to 9.8%) occurred in spring. Protein, which made up from 42.0% to 51.6% of the dry weight, followed a reverse seasonal variation

Table 3. Energy value of selected bivalve species from different coastal waters of subtropical and tropical regions. *N*: number of data. The number given in brackets is the mean.

Species	Location	Unit (kJ g^{-1})	Energy value	Method of determination	Sampling period	*N*	Reference
Perna perna	Gulf of Aden	ADW[a]	11.8–14.7 (13.7)	Microbomb calorimeter	July-Dec.	6	this study
		ADW	16.5–18.4 (17.5)	Conversion factors			
Perna perna	Moroccan Atlantic coast	AFDW	22.3–22.4 (23.2)	Conversion factors	Feb.-Jan.	19	Shafee (1989)
Perna perna	Brazilian Atlantic coast (near São Paolo)	ADW[b]	17.3–18.1 (17.7)	Atwater conversion factors	Jan.-Dec.	12	Tavares et al. (1998)
		AFDW[b]	19.1–19.4 (19.4)				
Perna viridis	Hong Kong coastal waters	DW	22.8	Oxygen bomb calorimeter	Sep.	1	Cheung (1993)
Perna perna	The Natal coast, South Africa	DW	14.6	Recalculated from energy budget	na	na	Berry and Schleyer (1983)
Perna (*Mytilus*) *viridis*	Goa, east coast of India	DW[b]	12.6–17.7 (13.9)	Conversion factors	Nov.-Oct.	12	Wafar et al. (1976)
Perna viridis	Karachi, Pakistan coast of the Arabian Sea	DW[b]	20.6–22.4 (22.0)	Conversion factors	Jan.-Dec.	12	Fatima (1996)

[a]ADW: ash dry weight; AFDW: ash free dry weight; DW: dry weight.
[b]Recalculated from kcal, using a standard conversion factor 1 kcal = 4.1868 kJ.

pattern to that of lipid (Spearman's rank correlation analysis, $p < 0.019$), with elevated values throughout winter and spring, and a lower level in summer and autumn (Fig. 3). A less pronounced temporal cycle was shown for ash content, whose contribution to mussel dry weight varied between 8.6% and 15.2%. Overall, the mineral content of *P. perna* was low in early autumn and late winter but increased in summer and spring, which can be explained, at least in part, by the concomitant changes in biochemical constituents.

The measured soft tissue energy value of *Perna perna* varied from 11.8 kJ g^{-1} ADW to 14.7 kJ g^{-1} ADW, corresponding to a range of 16.5 kJ g^{-1} ADW to 18.4 kJ g^{-1} ADW when estimated from the biochemical components using the standard conversion factors (Table 3).

3.3 Reproductive cycle and sex ratio

Gonad development in *P. perna* followed a clear annual cycle with peak activity over summer (August-September) and spring (March-April), and relative inactivity from November to February. The major spawning occurred in late summer (July-August, i.e. just before the SW monsoon) when up to 44% of the population were classified as spawning (stage IV) and 11% as spawning/resting (stage V) (Fig. 4a). Gametogenesis diminished considerably during the colder autumn and winter months (November-February). The second breeding event took place in early spring (at the end of the NW monsoon), as indicated by a high percentage of individuals spawning (24% in March). Remarkably, as much as 17% of the mussels remained in the ripe stage (III) throughout the whole study period.

The percentage contributions of the sexes appeared to be skewed in favour of males, which represented on average 52.1% of the samples, while females and undifferentiated mussels made up 29.5% and 18.4%, respectively (the disparity differed significantly from equality; χ^2 test, $p < 0.001$). The predominance of males was even more pronounced when the undifferentiated individuals were excluded from the calculation, females were then strongly outnumbered by males at a ratio of 1.8:1.00 males:females, corresponding to percentage contributions of 64% males and 36% females. There was temporal variability in the proportions of male, female and undifferentiated mussels (Fig. 4b) with males dominating notably in spring months (up 4.7:1.0 males:females) but an almost equal

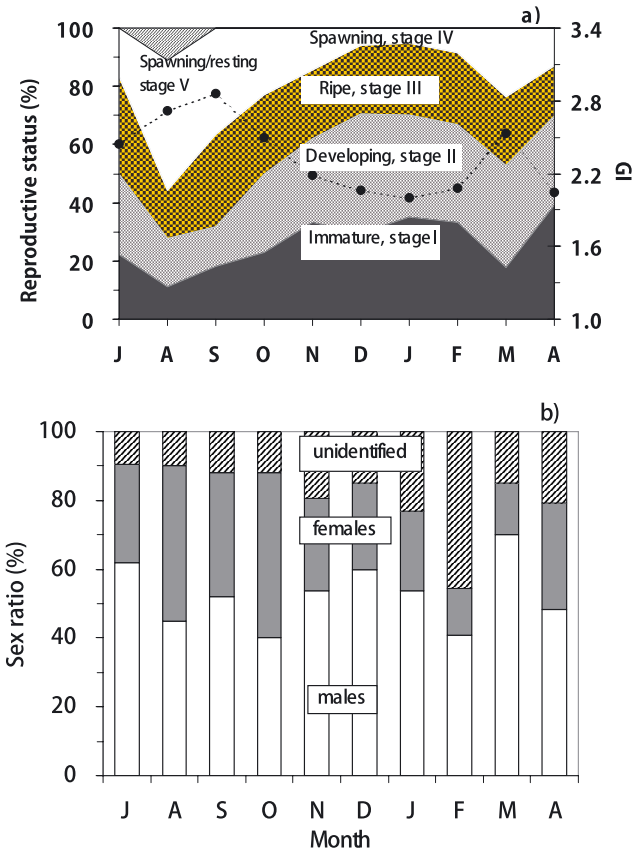

Fig. 4. Seasonal variations of gonad development and gonad index (GI) (a) and sex ratio (b). Dashed line: gonad index (scaled according to the right-hand y axis).

sex ratio (1.1) in summer. Out of a total of 221 individuals examined for sex, only two hermaphrodites were recorded.

3.4 Relationship between physiological-biochemical measures and environmental parameters

Results of the Multiple Regression Analysis, performed on physiological and biological measurements on *P. perna* and environmental data, showed the effect of water temperature, salinity, concentrations of oxygen and chlorophyll *a*, and particulate organic matter. Gonad index was positively correlated with salinity ($p < 0.01$) and chlorophyll *a* ($p < 0.05$), and negatively correlated with temperature ($p < 0.05$) and dissolved oxygen ($p < 0.01$). In contrast, POM was negatively correlated with lipid and individual soft tissue dry weight (both $p < 0.05$) while chlorophyll *a* was negatively correlated with protein ($p < 0.05$). No significant multiple regression correlations were found for carbohydrate, glycogen, ash, body wet weight, or the condition indices.

4 Discussion

4.1 Ecophysiological performance of *Perna perna*

The brown mussel *P. perna* is widely distributed along the coastline of the Gulf of Aden and often constitutes a dominant sessile epifauna on exposed rocky platforms and gravel sediments in the intertidal and shallow sublittoral zones (Bawazir 2000). Wild mussel populations can thus offer an important easy-accessible protein-rich food resource for domestic consumption, while the species may have potential for commercial cultivation in the highly productive area of the Hadramaut district.

The annual cycle of ecophysiological performance in *P. perna*, with two spawning periods and inter-monsoon gametogenic quiescence and energy accumulation, broadly corresponds to that of closely related *Perna viridis* from the east coast of India (Rajagopal et al. 1998a), the coastal waters of Singapore (Low et al. 1991) and Hong Kong (Cheung 1993). However, reproductive and energy storage behaviour of the brown mussel along the Yemeni coastline is distinct from other subtropical representatives of the genus (Rajagopal et al. 2006), reflecting particular ecological features of the bivalves and hydrological regime in the Gulf of Aden. The two bouts of spawning (late summer and early spring) differ considerably in relative intensity and extent of subsequent changes in soft tissue composition and body weight. The major breeding season, in terms of a number of individuals in the final gametogenic stages (IV and V), was observed in August-September, when the frequency of spawning and spawning/resting mussels reached 55.6% of the total population. Spawning in late summer coincided with low water temperature and high salinity due to upwelling of colder and nutrient-rich water masses during the SW monsoon. Enrichment of surface euphotic water with nutrients favoured phytoplanktonic primary production, leading in consequence to a marked increase in trophic resources in the water column at that time. Hydrological variables, namely temperature, salinity and nutrition (food availability), seem to initiate the main reproductive activity of *P. perna*, as was also observed for *P. viridis* in other subtropical areas (Rajagopal et al. 2006). However, the degree to which a given abiotic factor can affect gonad maturation in pernids varies considerably with species and geographical region. The summer release of gametes resulted in a substantial decline of individual tissue weight and weight index CI1 (Fig. 2), indicating ~ 30% reproductive output i.e. much higher than the mean annual gonad output calculated for *P. perna* (13%) in the coastal waters of southern Africa (van Erkom Schurink and Griffiths 1991). Surprisingly, large reproductive investment of the brown mussel during the summer spawning induced only a slight reduction of lipids, which form the main component of reproductive material (Zandee et al. 1980) as high-energy reserves for future larvae in the early stages of life. Accordingly, glycogen, which also serves as an energy source for gamete maturation, decreased slightly, while total carbohydrates even rose over the same period (Fig. 3). Enhanced energy demands of spawning were covered mostly by energy acquisition from phytoplanktonic food. Alternatively, the protracted release of low numbers of small eggs and sperm in small portions would have a limited effect on gross lipid and glycogen contents, providing another explanation. In addition, under conditions with abundant food, planktonic mussel larvae might contain less lipid reserves and rely more on external energy resources. According to Rajagopal (1991), the abundance and growth of mussel larvae in the coastal waters is linked to sufficient food availability, which enhances the chance of larval development and successful settlement. Since a relatively large fraction of the adult population (17%) was ripe throughout most of the year, it cannot be excluded that *P. perna* breeds in minor but numerous events that are not well isolated and occur over many months, as has been already reported for the brown mussel in southern Africa (Lasiak 1986; van Erkom Schurink and Griffiths 1991). Multiple intermittent spawning has been often observed in ecosystems where the resident mussels live under environmental stress, including stress from the thermal regime, prolonged aerial exposure and restricted productivity e.g. in the upwelling area (Griffiths 1977) or in eutrophicated water-basins (Newell et al. 1982; Wołowicz et al. 2006). It has been therefore hypothesized that under adverse hydrological conditions, e.g. high temperature, the ecophysiological strategy of *P. perna* may be that a portion of the population is able to spawn over extended time. A continuous dribble of spawning was suggested as a strategy to ensure that in adverse environmental situations that could reduce or prevent settlement of larvae, only a small proportion of potential mussel recruits would be lost (Newell et al. 1982).

Over the inter-monsoon period of September-November and at the beginning of the NW monsoon, energy reserves (lipids, carbohydrates, and glycogen) and, to a limited degree protein, built up as water temperature dropped and phytoplanktonic food remained fairly abundant (Fig. 3). Accumulation of biochemical components induced a gradual increase of individual soft tissue dry weight and the consequent increase of condition indices (Fig. 2). After the main spawning in summer, gonad activity decreased, although ~ 25% of the population was still ripe. In autumn/winter months, energy acquired from food was allocated mainly into reserve storage and somatic tissues to provide energy for periods of natural nutritional stress

when water temperature increased and primary production diminished (Shafee 1989; Narváez et al. 2008).

An increase of gonad index in early spring indicated the second breeding season at the end of the NE monsoon period when water temperature, salinity and food availability were relatively low. Despite the notably lower intensity (only 23.5% contribution of individuals in the IV and V gametogenic stages) the spring reproductive event exerted a much more pronounced effect on the ecophysiological performance of *P. perna*. In contrast to the summer spawning, spawning in spring induced a substantial decrease in lipids, carbohydrates and glycogen, suggesting elevated metabolic energy demand. Gametes were probably released at the expense of the mussel's endogenous energy reserves, which declined in total body weight over this time, suggesting ~ 28% reproductive effort. In response to the limited food abundance and quality in the external environment, mussels may produce numerous and large eggs of high lipid content to provide sufficient energy during embryogenesis and metamorphosis, thus increasing offspring fitness (Bernardo 1996). Greater allocation of energy from parental resources into lipid and carbohydrate reserves of gonads in spring can thus be an adaptive strategy to scarcity of food in the water column during the NE monsoon. Further support for the concept of a large breeding-induced energy expenditure of *P. perna* in spring is provided by the percentage contribution of the sexes, which was notably skewed in favour of males during spawning (Fig. 4b). The ecological significance of the biased sex ratio has been considered to reflect the greater reproductive effort of females, which produce much larger gametes than males per unit of reproductive output (van Erkom Schurink and Griffith 1991). Given the similar amounts of spawned gametes in terms of weight by the two sexes (Thompson 1979) and higher caloric value of eggs relative to sperm, gamete release in females leads to a stronger decline in body weight. In extreme cases, when energy demands are in excess of available reserves and energy acquisition from food, this can cause the death of an organism (Bayne and Newell 1983).

4.2 Ecological physiology of mussels and environmental parameters

In the subtropical ecosystem of the Gulf of Aden, water temperature and food availability and quality appear to be the crucial abiotic factors affecting ecophysiological performance of the brown mussel. Salinity only varies within a narrow range and its effect is less discernible. The degree to which a given environmental parameter governs metabolic activity of the brown mussel in the Yemeni coastal waters differs among seasons, however. While low water temperature may induce general metabolic activity throughout the year, including reserve storage, gonad development and spawning, food abundance may influence energetic investments of an organism into somatic growth and gonads to optimise reproductive success during subtropical monsoons. The main breeding in summer is likely initiated by elevated food supply and a decline in water temperature down to 24.4 °C in July due to upwelling of cold and deep waters in the SW monsoon period. Similarly, Lunetta (1969) reported that spawning of *P. perna* occurred when temperature declined from 28 °C to 22 °C and Vélez and Epifanio (1981) and Shafee (1989) observed gamete ripening and release in the same species at water temperatures of 21 °C and 15 °C, respectively. During the intermonsoon months in autumn, when temperature remained low and POM fairly high, the bivalves stored lipid and carbohydrate energy reserves to recover after spawning and develop gonads. The second spawning event occurred just before mussels experienced water temperature above 26.0 °C in spring and was associated with the increased inorganic seston at the end of the NS monsoon. Inversely, high water temperature may have inhibited gametogenesis. This agrees with the thermal control of reproductive pattern in *P. perna* from Mexico (Vélez and Epifanio 1981) but contrasts with the spawning activity of closely-related *P. viridis* from the east coast of India, the breeding of which coincides with seasonally elevated temperatures up to 31.3 °C (Rajagopal et al. 1998b). Synchronisation of spawning and an adequate food supply in the surrounding water has been suggested in brown mussels from various subtropical and tropical regions e.g. in India (Rajagopal 1991; Rajagopal et al. 1998a), Singapore (Low et al. 1991), Japan (Yoshiyasu et al. 2004) and Venezuela (Narváez et al. 2008).

4.3 Inter-regional comparison of tissue energetic value

In relation to other bivalves in the large-scale geographical comparison of the soft tissue energetics (Table 3), the brown mussel from Yemen demonstrated an intermediate value, indicating its good potential for use as a protein-rich resource for domestic consumption and in aquaculture. Although the brown mussel demonstrates narrower thermohaline tolerance and capacity for adaptation to alterations of hydrological parameters than other pernids (e.g. the green mussel *P. viridis*; Rajagopal et al. 2006), *P. perna* from the Yemeni coastal waters shows good environmental fitness. Its physiological cycle and efficient utilization of available energy resources enable the mussel to grow rapidly, sustain periods of adverse conditions and reproduce successfully.

Acknowledgements. This research was supported in part by a grant (to A.S.B.) from the Yemeni government represented by Aden University and Hadramaut University for Science and Technology.

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