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ECOLOGICAL ENERGETICS OF TROPICAL LIMPET *Cellana testudinaria* (Linnaeus, 1758) LIVING ON THE ROCKY SHORE OF OHOIWAIT, SOUTHEAST MOLUCCAS, INDONESIA

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ABSTRACT

Study on ecological energetics of tropical limpet C. testudinaria has been carried out at approximately one year from October 2001 to September 2002. Population energy budgets estimated on the assumption of steady state conditions for C. testudinaria (Linnaeus, 1758) on the rocky shore of Ohoiwait, are presented. Large difference in population structure, and hence energetics, occurred at different localities along the rocky shore. Relatively high proportions (98 %) of the assimilated energy was lost via metabolism. Assimilation efficiency is 39 %, net growth efficiency is 1.8 %, and ecological efficiency 0.3 %. Production (P), energy flow (A) and total energy consumption (C) were expressed as functions of animal size, in order to facilitate gross estimations of the energy component for which data on size frequency and density are available.

Key words: *ecological energetics, cellana testudinaria, energy components*

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INTRODUCTION

Cellana testudinaria is intertidal, grazing gastropod abundant on medium to very exposed rocky shores of Ohoiwait. The species shows marked zonation, with only a little overlap between zones. *C. testudinaria* occurs at several spatial and temporal scales from the extreme low water spring tide (ELWST) to the extreme high water spring tide (EHWST) and above EHWST in more exposed situation, where it is almost continually splashed by wave action but seldom actually submerged. Tide of Ohoiwait's intertidal is mixed tide prevailing diurnal type, with the average "spring" of about 1.5 m and "neap" of about 1 m.

Little has been published on the ecology of *C. testudinaria*. Khouw (2002) discussed their growth pattern and shell shape variation in relation to zonal distribution. Distribution, abundance, and biomass were investigated by Khouw (2006a) and presented evidence for the effects of drying. For several years, the recruitment pattern and productivity of this species have been studied at the rocky shore of Ohoiwait (Khouw, 2005; 2006b). Work has also been done on the growth determination of this species (Khouw, 2007).

The purpose of the study presented here was to augment the data on growth rates, spawning and respiration with further observations on population structure, defaecation rates and the caloric contents of tissues and faeces, in order to compile population energy budgets for *Cellana testudinaria* on the rocky shore of Ohoiwait.

MATERIALS AND METHODS

Study site

The study was carried out on the intertidal rocky shore of Ohoiwait (latitude $5^0$45'15" S, longitude $132^0$57'20" E), Big Kai Island, Southeast Mollucas, Indonesia **(Fig. 1)** from October to November 2007. The intertidal region investigated is about 0.25 km^2 (1 km long and 0.25 km wide). Thus, it is small enough that atmospheric conditions may be assumed, for most purposes, to be uniform over the whole area. The shore consisted of singles, pebbles, medium and big boulders of about 90% of covering substrate. The physical conditions in the tidal zones are quite different; the higher shore is wetted almost exclusively by tidal sea level rise, but the lower shore receives considerable wave action.

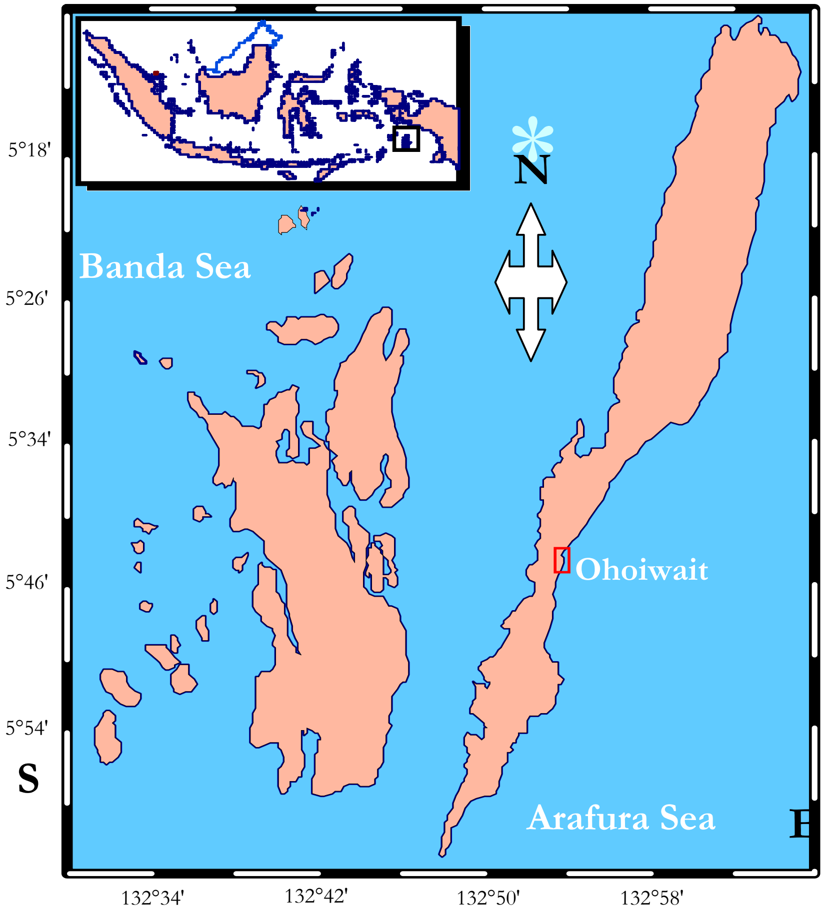

Fig 1. Map of study site of Ohoiwait located at the Big Kai Island.

Population structure

Population of *Cellana testudinaria* was studied at the rocky shore of Ohoiwait, where previous work had been done on the distribution, abundance, and biomass of this species (Khouw, 2006b). The rocky shore of Ohoiwait, described in detail by Khouw (2003), is exposed to prevailing south-northly monsoons, therefore, the perpetual "dry" season which is characterized of daily maximum insolation and minimum humidity and precipitation.

Density of species varied enormously, even within short distance (10 m), along the shore. Topography seemed to be the main cause of this heterogeneity. Population samples were taken from small areas of shore having a fairly uniform topography. Acquisition of data sufficient for population estimates over larger areas of shoreline was beyond the scope of this study. *C. testudinari*a occupied a well defined zone, which was sampled throughout its 25 m wide range by six 1 m^2 continuous quadrats forming a square with sides of 3 m.

Energy Budget

The population energy budget may be represented by the equation: $C = P + R + F + U$ where $P = P_g + P_r$, $P_g = \Delta B + E$, and $P + R = A$. The terminology is that recommended by Chislett (1969). All the components may be expressed as Kcal/m^2/year. C is the total amount of energy consumed by the population; production (P) comprises energy added to the population by growth and recruitment (P_g), and the energy released as spawned gametes (P_r). P_g is also equal to the sum of ΔB, the net increase or decrease in the standing stock of the population, and E, the energy eliminated from the population due to mortality. R is the metabolic heat loss from the population, estimated from rates of oxygen consumption. F is the energy lost via the faeces and U is the energy lost via urine or other exudates. U is assumed to be negligibly small, and is ignored in this study. A is the energy flow through, or energy assimilated by the population.

Ideally, all components of the energy budgets should be estimated separately (Paine, 1971), to provide internal checks on their reliability. However, due to the nature of feeding, it was impossible to estimate *C. restudinaria* separately, and there were no data available for an independent estimate of mortality (E). An approximation was, therefore, made by assuming steady-state conditions and stable size-frequency structures of population. Steady growth rates and continuous spawning throughout the year perhaps lessen the error involved in these assumptions. Under steady-state condition $\Delta B = 0$ so that $P_g = E$. i.e., the estimate of production due to growth and recruitment (P_g) is assumed to equal the mortality (E).

Production (P)

Growth (P_g)

The equation used to estimate the annual growth in shell length was $L_t = L_\infty [1 - e^{-K(t - to)}]$ where L_t is the length at age t, L_∞ is the asymptotic length, K is the growth coefficient, and t_0 is the theoretical age at length 0 (Bertalanffy von, 1938).

The relationship between shell length and ash free dry weight (AFDW) was found by extracting limpets from their shell, removing the heavy calcareous operculum, drying for 48 hours at 70 °C and weighing to 0.1 mg. Regression equation with 95% confidence limits fitted to the data is: ln AFDW = ln a + b ln shell length.

Calorimetric determination was made by burning three approximately 1 g replicates, of the powdered tissue of the species, dried for 48 hours at 70 °C in an adiabatic bomb calorimeter (Parr Instrument Company, Illinois, USA). Ash contents were estimated by roasting the samples at 600 °C in a muffle furnace for 12 h. The calorific value of *C. testudinaria* (21.59 Kcal/g AFDW) was used to convert growth in biomass to energy increments (P_g).

Spawning (P_r)

C. testudinaria deposite their egg capsules on the rocks about mean tide level (MTL). Egg capsules tend to be laid in shallow water-filled depressions, underneath rocks, or where irregularities in the rock surface afford some protection from the sun.

For the purpose of computing P_r, Khouw (2003) figures 150 egg capsules/year for an "average" sized *C. testudinaria* was used. According to Khouw's size-frequency data, the length of the average sexually mature individual was 30 mm.

To determine calorific value, *C. testudinaria* egg capsules were carefully scraped from building bricks on which they had been laid, and examined for rupture of the lower wall. Only intact capsules were used (about 25%). The calorific value of four replicates, each of 20 capsules, was estimated by wet oxidation with potassium iodate in sulphuric acid. The mean with 95% confidence limits was 4.41 ± 0.36 cal/capsule.

Gonad weight, and hence gamete production, was assumed to be a function of the cube of the shell length. On this assumption, the calories produced per animal per year as gametes may be expressed as a function of shell length (mm) by the following equation: Ln gamete production = 3*ln shell length – a.

Respiration (R)

Limpets collected from the field were kept in running seawater at about 30 ^oC overnight, during which time they voided most of the faeces. Scholander manometric respirometers manufactured by (the Mark Company, Randolph, Massechusset, USA) were placed in a constant-temperature bath at 30.4 ± 0.05 ^oC. Sets of 10 limpets, one in each respirometer were kept in the respiration chambers for 1 hour before commencing the experiments. The means of 4 consecutive hourly readings were taken, and the shell length of limpet measured to the nearest 0.1 mm.

Defaecation (F)

Limpets collected at dawn were placed on native rock in glass fingerbowls in the laboratory. Seawater came to a level halfway up the rock, and a perspex cover prevented individuals from escaping. Faecal pellets were collected 24 hrs later, briefly washed in tap water to remove sea salt, dried for 24 hrs at 70 ^oC, and weighed to 0.1 mg. Shell lengths of the limpets were measured to 0.1 mm. Equation with 95 % confidence limits relating faecal production (mg/limpet/24 hrs) to shell length (mm): Ln dry weight faeces = Ln shell length + a.

Calorific values of faeces were estimated by wet oxidation with potassium iodate in sulphuric acid. Energy lost as faeces (*F*) from the population was estimated from size-frequency data, the relationship between rate of faecal production and size, and the calorific values.

RESULTS AND DISCUSSION

Results

Population Structure

The size class structure of the population of *C. testudinaria* was studied through the analysis of percentage size frequency distribution **(Fig. 2)**. The 2402 collected specimens ranged in length from 8.2 to 31.8 mm with an average of 16.22 ± 5.26 mm while their total body wet weight varied between 0.11 and 4.93 g with an average of 0.55 ± 0.70 g (Khouw, 2007).

The distribution was markedly bimodal (2 cohorts), with a greater excess of

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the larger density at the small size group (12.5 – 14.5 mm) and a slight excess of the smaller density at the big size group (24.5 – 26.5 mm). Since limpets could not be aged, it is impossible to say whether the differences in size-frequency structure of the *C. testudinaria* population was due to growth conditions, or whether the sub-population (cohort) after some previous increasing in size was in phase of recovery and would eventually resemble the other sub-population.

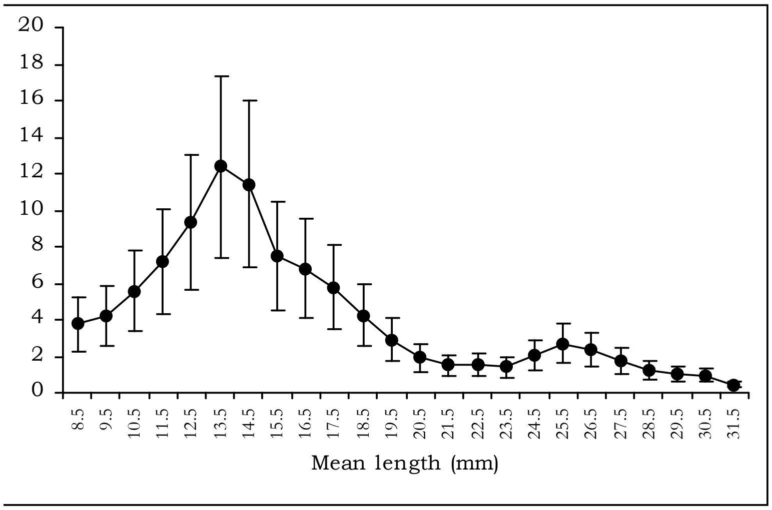

Fig 2. *Cellana testudinaria*. Mean percentage frequency of each size class category. Vertical lines represent standard deviation

Growth (P_g)

The von Bertalanffy equation of *C. testudinaria* (Khouw, 2007) used to estimate the annual growth in shell length was $L_t = 33.08\ [1 - e^{-1.4(t\ +\ 0.09)}]$. From this equation, the shell length of limpet at the age of 1 year old is 25.80 mm. The 95 % confidence limits of the relationship between shell length and total body wet weight for the whole period of study was $WW = 0.0002343(\pm\ 0.000031)\ L^{2.6601(\pm\ 0.0454)}$ **(Fig. 3)**, hence 95 % confidence limits of the relationship between ash-free dry weight (mg AFDW) and total body wet weight (mg WW) was $AFDW = 0.03236(\pm\ 0.0178)\ WW^{2.7703(\pm\ 0.3813)}$ (Khouw, 2006b). It was, therefore, found that the calorific value (P_g) of *C. testudinaria* was 1.55 Kcal/m^2/year.

Spawning (P_r)

Using Khouw (2007) figures, a 25.80 mm female *C. testudinaria* and the relationship equation of Ln gamete production = 3 ln shell length – 4.4642 (Khouw, 2003) was estimated to produce 197.73 cal/year. The calorific value (P_r), therefore, was estimated to be 0.87 Kcal/m^2/year. Summing the values for P_g and P_r, the figures for total production, P, is 2.42 Kcal/m^2/year.

Respiration (R)

Energy lost as heat from the population due to metabolism was estimated from respiration rates measured in the laboratory. Oxygen consumption rate was converted to heat production by multiplying by an oxycalorie coefficient which assumes that, when carbohydrate fat and protein are completely burned in 1 ml of oxygen at normal temperature and pressure (NTP), an average of 4.89 cal are released (Sutherland, 1972; Wright & Hartnoll, 1981; Workman, 1983). The appropriate equation: Ln µl O_2/ind./hr = 0.7206 ln wet flesh weight (WW) + 0.1569. The mean respiration rates, therefore, obtained in this study was 217.3 Kcal/m^2/year.

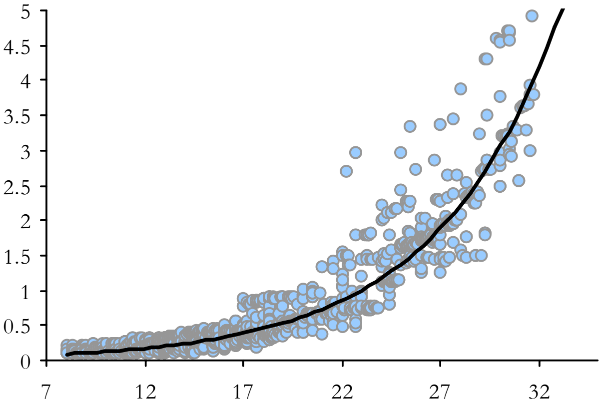

Fig 3. *Cellana testudinaria*. Relationship between shell length (L) and total body wet weight (WW) (Khouw, 2006b).

Defaecation (F)

Regression fitted to the data suggest that faecal production is roughly proportional to the square of the shell length. Equation with 95% confidence limits relating faecal production (g/limpet/24 hr) to shell length (mm) is: Ln dry weight faeces/ind./24 hrs = 1.6950 (± 0.3584) ln shell length – 3.9989 (± 0.3178). The 95% confidence limits of calorific value of the faeces, therefore, were estimated by wet oxidation with potassium iodate in sulphuric acid to be 287.1 (± 25.5) cal/g. Energy lost as faeces (*F*) from the population was estimated to be 351.4 Kcal/m^2/year.

Energy Budget

Summation of the components estimated above complete the population energy budget in Kcal/m^2/year as follows: (1) $P = P_g + P_r = 1.55 + 2.42 = 3.97$, (2) $A = P + R = 3.97 + 217.3 = 221.27$, and (3) $C = A + F = 221.27 + 351.4 = 572.67$. The proportion of energy assimilated which is lost via metabolism (R/A x 100%) is 98%, the assimilation efficiency (A/C x 100%) is 39%, the net growth efficiency (P/A x 100%) is 1.8%, and the ecological efficiency (E/C x 100%) is 0.3%.

Discussion

Compared with many other invertebrates (Sutherland, 1972; Picken, 1980; Parry, 1982; Workman, 1983; Blankley & Branch, 1985), the *Cellana testudinaria* is estimated to lose a high percentage of assimilated energy via metabolism. A similarly high estimate of assimilated energy lost via metabolism (95%) was given by Wright & Hartnoll (1981) for *Patella vulgata*, which is also an intertidal gastropod browsing on detritus and algae.

Williams & Morritt (1995) suggested that long live poikilotherms, where a proportion of the population is in excess of two years old, lose more of assimilated energy via heat loss. Such animals are supposed to experience high respiratory cost, non-productive periods, e.g. *Cellana grata*, during summer at lower latitudes or during aestivation, so that annual production efficiencies are low. Limpet *C. testudinaria* species falls into this category.

Net growth efficiency of *C. testudinaria* was relatively low (other invertebrates range from 11 to 73 %; Branch, 1981), and may have been due to slight underestimations of growth rates by von Bertalanffy equation. In general, there is a strong positive correlation between growth and production. Somatic growth (P_g) can be reduced in favor of reproductive effort (P_r), as it has been showed by Branch (1981) for seven South African *Patella* species. However, overall the growth rate was positively correlated with the reproductive effort. This implies that although energy may be diverted from P_g to P_r (or *vice versa*) when food is short, in general species have "strategies" of high or low turnover (Branch, 1981).

The assessment of the energy content calculated for the limpet *C. testudinaria*, gives a value of 21.59 $kJ.g^{-1}$ AFDW. This value was considerably higher than that of many temperate limpet species, such as *Patella vulgata* (19.3 $kJ.g^{-1}$ AFDW) (Workman, 1983), and *Nacella delesserti* (20 $kJ.g^{-1}$) (Blankley & Branch, 1985), but eventually similar to the tropical limpet species such as *Cellana tramoserica* (22.59 $kJ.g^{-1}$), *Notoacmaea petterdi* (21.63 $kJ.g^{-1}$), *Patella peroni* (22.30 $kJ.g^{-1}$), and *Patelloida alticostata* (22.93 $kJ.g^{-1}$) (Parry, 1982). An attempt to present the species energy budgets in a more useful way was made by expressing production (P), assimilation or energy flow (A) and total energy consumption (C) as functions of animal size.

CONCLUSION

This study establishes a baseline for ecological energetics of *Cellana testudinaria* living on the rocky shore of Ohoiwait. Large differences in population structure, and hence population energetics of this species occurred at different zones along the shore. The proportion of assimilated energy lost via metabolism was rather high (98%) but comparable to the intertidal limpet *Patella vulgata* (95%) studied by Wright & Hartnoll (1981). Assimilation efficiency (39%) was higher but net growth efficiency (1.8%) was lower compared to others intertidal limpets 11-73% studied by Branch (1981), while ecological energetics was 0.3%.

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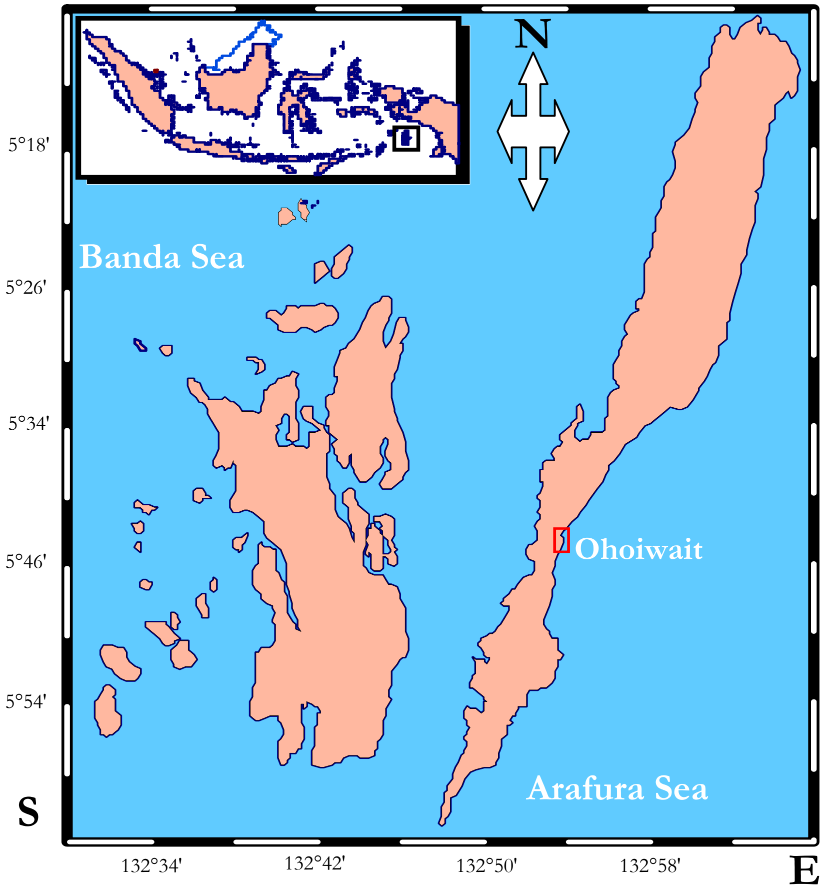
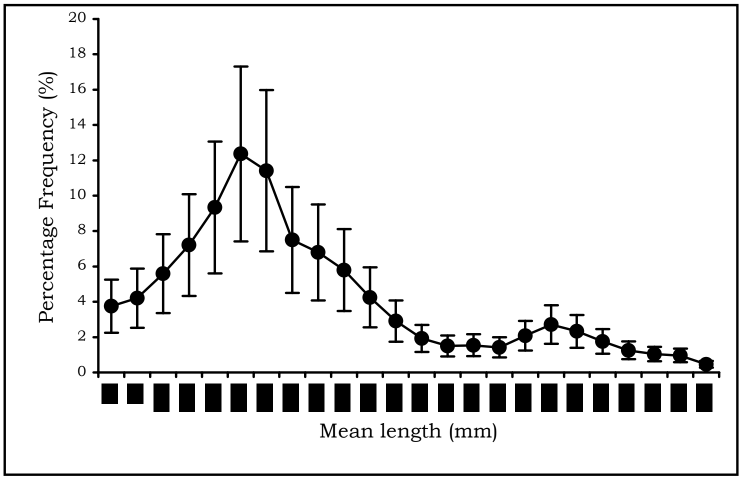


Figure 1. Map of study site of Ohoiwait located at the Big Kai Island.



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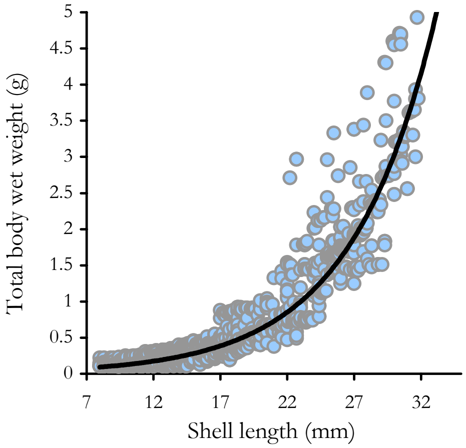

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