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Distribution, Abundance, and Biomass of Tropical Limpet *Cellana testudinaria* (Class: Gastropoda, Family: Patellidae) Living on the Rocky Shore of Ohoiwait, Southeast Moluccas, Indonesia

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Abstrak

Distribusi, kelimpahan, dan biomassa dari limpet C. testudinaria digambarkan secara terpisah untuk zona pantai bagian atas, tengah, dan bawah. Total 2402 ekor limpet diperoleh selama 12 bulan (dari Oktober 2001 sampai 2002). Rata-rata densitas adalah 11.12 ± 4.51 ind.m^{-2}. Densitas tertinggi berada pada zona atas dan tengah daripada zona bawah. Analisa varian menunjukkan perbedaan nyata antar zona, bulan, dan interaksi zona-bulan. Pola penyebaran limpet adalah berkelompok. Rata-rata biomass tahunan diestimasi sebesar 1013 ± 748 mg AFDW.m^{-2} (21.8 kJ.m^{-2}). Biomassa tertinggi 3236 mg AFDW.m^{-2} atau 69.9 kJ.m^{-2} ditemukan pada bulan September 2002, sementara terrendah pada bulan Maret 2002 sebesar 544 mg AFDW.m^{-2} atau 11.7 kJ.m^{-2}. Rata-rata biomassa pada musim hujan 619 mg AFDW.m^{-2} atau 13.4 kJ.m^{-2} lebih rendah dibandingkan pada musim kemarau yakni 899 mg AFDW.m^{-2} atau 19.4 kJ.m^{-2}.

Kata kunci: *Limpet, Cellana testudinaria, distribusi, kelimpahan, biomassa*

Abstract

The distribution, abundance, and biomass of the tropical limpet C. testudinaria are described separately for the high, middle and low shore levels. A total of 2402 limpets were obtained in 12 monthly collections (from October 2001 to September 2002). The mean density over the whole period was 11.12 ± 4.51 ind.m^{-2}. The density tended to be higher at the high (15.79 ± 7.54 ind.m^{-2}) and the middle (14.67 ± 13.99 ind.m^{-2}) than at the low shore level (2.90 ± 2.44 ind.m^{-2}). Analysis of variance showed significant density differences among shore levels, months, as well as a significant interaction between shore levels and months. The small-scale dispersion patterns did not show any seasonal variability. They were strongly clumped throughout the year and at each shore level. The mean annual population biomass was estimated to be 1013 ± 748 mg AFDW.m^{-2} (21.8 kJ.m^{-2}). The highest biomass (3236 mg AFDW.m^{-2} or 69.9 kJ.m^{-2}) occurred in September 2002, whilst the lowest (544 mg AFDW.m^{-2} or 11.7 kJ.m^{-2}) was in March 2002. The monthly mean biomass (619 mg AFDW.m^{-2} or 13.4 kJ.m^{-2}) of the rainy season was lower than that (899 mg AFDW.m^{-2} or 19.4 kJ.m^{-2}) of the dry season.

Key words: *Limpet, Cellana testudinaria, distribution, abundance, biomass*

Introduction

Natural assemblages of species are inherently variable (Menconi *et al*., 1999). Changes in the composition and abundance of organisms occur at several spatial and temporal scales (Barry & Dayton, 1991; Menconi *et al*., 1999). This variability was primarily explained by the effects of abiotic parameters and resources availability in the environment in relation to physiological traits of the species (Stephenson & Stephenson, 1972; Underwood, 1979). However, several authors reported an increasing body of evidence for the importance of biotic factors such as competition and predation (Paine, 1974; Underwood, 1979). Recently, there is increasing evidence from different areas of ecology for the notion that patterns in nature are influenced by both abiotic and biotic factors (Schneider, 1994; Wu & Loucks, 1995). A number of processes have been invoked to explain natural patterns, including behavioural effects and small-scale changes in the topography of the substratum (Underwood & Chapman, 1998; Benedetti-Cecchi *et al*., 2000).

Rocky coastlines are heterogeneous environments supporting variable assemblages of sessile and mobile organisms. A prominent feature of these systems is that species generally occur at some levels on the

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shore but not at others. Limpets, which occupy both intertidal and intratidal habitats, have a high relative abundance on most hard substrata in shallow (Liu, 1994). Many studies on rocky coasts have focused on the seasonal changes and the factors influencing the distribution and abundance of limpets (see review by Branch, 1981). These factors include physical conditions related to desiccation, temperature, salinity, and light (Balaparameswara Rao & Ganapati, 1971; Liu, 1994), wave action (Jones & Demetropoulos, 1968; Denny, 1985), tidal levels (Stephenson & Stephenson, 1949; Ebling *et al*., 1962). The vertical patterns in the distribution (zonation) are thought to be primarily caused in response to the major gradient of emersion and desiccation (Stephenson & Stephenson, 1949; Lewis, 1964). However, biotic interactions have also been described to affect limpet distribution. *C. testudinaria* as an intertidal limpet ranged freely on all rocky substrata at the intertidal of Ohoiwait. The individuals were abundant on bare rock outcrops and big encrusted boulders, but they were also found on small stones, gravel, pebbles, and shingles. The number of adults and juveniles on permanent substrata was also reasonably stable throughout the period of the study. Only little quantitative information is, however, available on the distribution and abundance of this species in Indonesia or elsewhere in the world (Powell, 1973).

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 2001 to September 2002. 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 shingles, pebbles, medium and big boulders. 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.

Sampling

Fieldwork was undertaken at the intertidal rocky shore of Ohoiwait between October 2001 and September 2002 (Table 1). Three different tide levels (from the extreme high water spring tide EHWST to the extreme low water spring tide ELWST) parallel to the shoreline (Fig. 2) were defined in relation to heights above the mean low water level predicted by local tide tables (Dinas Hidro-Oseanografi TNI AL, 2001; 2002). These zones were identified using staffs and a spirit-level during calm days. In the following, they are high (1 – 1.5 m), middle (0.5 – 1 m) and low (0 – 0.5 m) shore levels. The width of each shore level ranges from 80 m to 85 m (Fig. 2).

As pure random sampling was not feasible due to pronounced environmental heterogeneity within the shore levels, a systematic sampling design was chosen. At each shore level, 6 sampling squares (1 m^2), 25 m apart, were installed along a line parallel to the shoreline. Hence, a total of 18 permanent quadrates were placed between the EHWST and the water edge, the first square being randomly defined. Heights of the quadrates above ELWST and the distances between quadrates were calculated from the profiles obtained.

In each quadrate, adults (> 25 mm), juveniles (> 10 mm and < 25 mm), and recruits (< 10 mm) were collected by hand picking or dug out with a spade, and the shells were cleaned from the material covered. Sampled specimens were counted and measured for their shell dimensions using vernier calliper to the nearest 0.1 mm, while their total body wet weights were weighed using an analytical balance to the nearest 0.01 g, as this allowed limpets to be measured *in situ* on the shore. In some cases, the juvenile limpets could not be dug out because of their soft and brittle shell. Therefore, their shell was measured directly by placing the vernier calliper to the shell. After measurements, limpets were released back to their habitats.

Most of *C. testudinaria* live attached to the surface of the substratum, although some of them were also found hiding below the boulders, pebbles, and shingles. Rocks lying within the quadrates, which were movable, were turned over and removed down to bedrock, and the undersides of rocks were searched as far as possible, so that concealed limpets were included in the count. Loose small gravel, a habitat sometimes favoured by small individuals, was also carefully searched.

Sampling was conducted monthly during low tide and continued until the samples represent the most complete series of data, so that all settled individuals are represented in accordance with their relative frequency in the population.

In addition to the quantitative samples taken to assess abundances and distribution patterns, 50 specimens of *C. testudinaria* encompassing an even size distribution of limpets within the range of the population (i.e. 15 individual of 8-15 mm length; 20

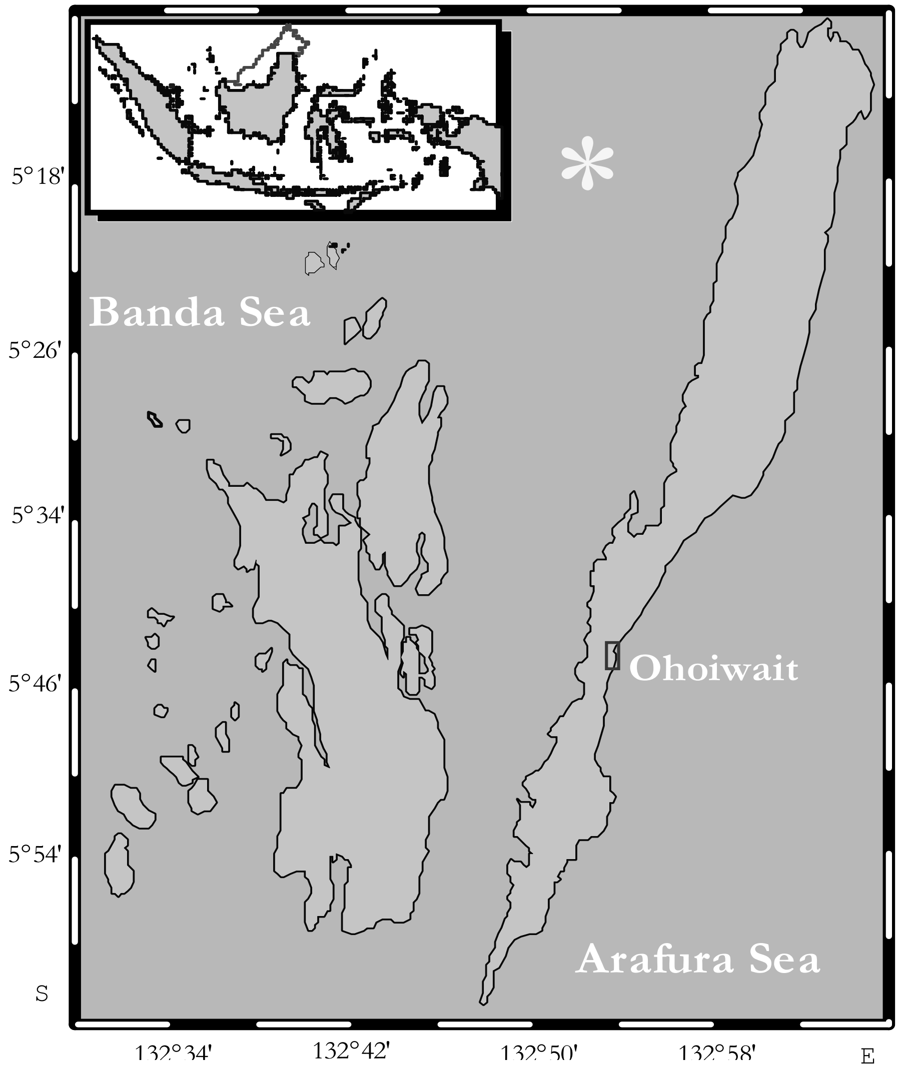


Figure 1. Map of study site of Ohoiwait located at the Big Kai Island

individuals of 15-25 mm; 15 individuals of >25 mm) were collected monthly for the determination of biomass and energy conversion factors. This standardization of the sample composition minimized the effect produced by "weight" samples on the results of regression analysis (Baxter, 1981). Their shell lengths were measured to 0.1 mm using vernier calliper.

Analyses

Distribution and abundance

Crossed two-way analysis of variance (ANOVA) was used to test the null hypothesis that "patterns in distribution and abundance of individual limpets did not change significantly between shore levels and months" (Morrisey *et al.*, 1992; Sokal & Rohlf, 1995; Underwood, 1997). Testing the null hypothesis model, I designed the comparison of vertical and temporal variability was designed using the factors shore level (3 levels) and sampling date (12 levels). This procedure resulted in independent estimates of variability for each level of shore (Searle *et al.*, 1992; Underwood, 1997). The assumption of homogeneity of variances was checked using Hartley's F_{max} test (Bakus, 1990; Sokal & Rohlf, 1995). Data transformation of log(X+1) was used.

The dispersion pattern of limpets in their habitat was assessed using the Morisita Index (Brower and Zar, 1977) $MI = [n(Óx^2) - n]/N(n - 1)$, where n is numbers of quadrates, x is number of individuals per quadrate, and N is total number of individuals. The dispersion can be contagious ($MI > 1$), random ($MI = 1$), or regular ($MI < 1$). This analysis was applied to determine whether environmental factors have any effect on the dispersion of the population, and whether

Table 1. Station list

Sampling dates		Numbers of limpets	Tidal state *	Moon phases	Season
03 October 2001	*(09:00 AM)*	394	± 50 cm	Full moon	Transition
03 November 2001	*(08:30 AM)*	216	± 38 cm	Full moon	Transition
05 December 2001	*(11:10 AM)*	137	± 23 cm	Last quarter	Rainy
02 January 2002	*(09:30 PM)*	146	± 23 cm	Last quarter	Rainy
03 February 2002	*(10:45 AM)*	171	± 45 cm	Last quarter	Rainy
04 March 2002	*(11:10 PM)*	129	± 45 cm	Last quarter	Transition
03 April 2002	*(10:00 AM)*	301	± 68 cm	Last quarter	Transition
05 May 2002	*(12:10 PM)*	161	± 83 cm	Last quarter	Transition
07 June 2002	*(17:20 PM)*	140	± 68 cm	Last quarter	Dry
05 July 2002	*(15:00 PM)*	165	± 68 cm	New moon	Dry
05 August 2002	*(16:08 PM)*	174	± 60 cm	New moon	Dry
05 September 2002	*(17:30 PM)*	268	± 53 cm	New moon	Transition

Note: * numbers refer to the water level above ELWST (as predicted from tide tables).

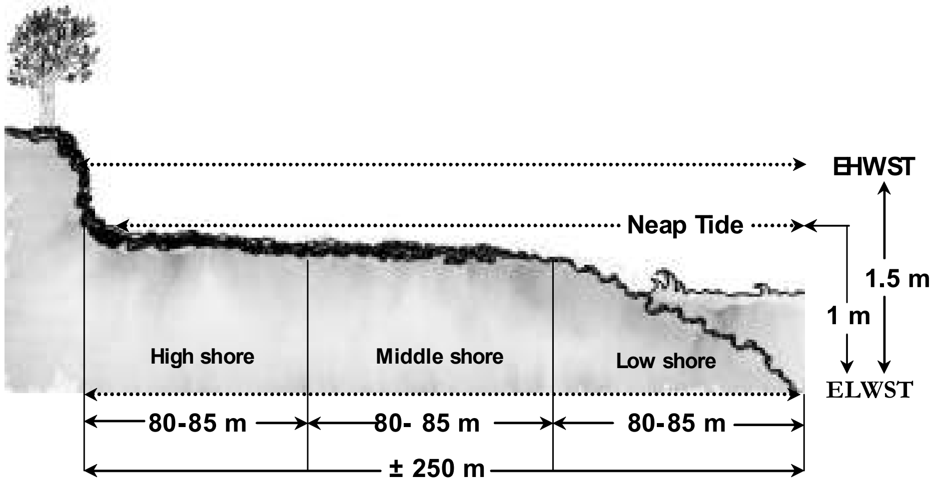


Figure 2. Intertidal rocky shore of Ohoiwait with schematic sketch of the tidal range.

there is no tendency for individuals in population to avoid or to move towards each other.

Biomass

The relationship between shell length (L, in mm) and total body wet weight of limpet specimen (WW, in g) was examined by testing the fit of pairs of variables to the allometric equation $Y = A\,X^b$, or, rewritten in logarithmic form $\ln Y = b \ln X + \ln A$, where y is the total body wet weight and x is the shell length. The constants b and A were estimated by least-squares regression. The variance of b was estimated using the equation $sb^2 = 1/(n-2) * [(sy/sx)^2 - b^2]$, where sy and sx are the standard deviation of y and x. Using a value of t from statistical table with $n - 2$ degree of freedom, the 95 % confidence limits were estimated as: $b = t * sb$. Students' t-test was applied to test the deviation of b from isometric (b=3).

The soft tissues of limpets sampled for determining biomass and energy conversion factors were removed from their shell and dried at about 60^{0}C for 3 days in an oven and finally vacuum-sealed in polythene bags. After transporting them to Ambon, samples were dried to constant weight at 108 ^{0}C. The total ash free dry weights (AFDW) of tissues were determined (accuracy 0.1 mg) by incinerating the sample in a muffle furnace at 500 ^{0}C for 12 h.

The energy content of the flesh was determined from a representative sample using a Gentry diabatic microbomb calorimeter. For each determination, at least 10 individuals were homogenised and the ash contents of 3 replicate samples and the energy contents of 4 replicate samples were measured.

The relationship between log total body mass (BM, in mg AFDW) and log shell length (L, in mm) were also calculated using least-square method (Sokal & Rohlf, 1995). Using this size-weight relationship in combination with the mean population densities and the mean body sizes, the mean population biomass was computed for each month.

Results and Discussion

Spatial and temporal patterns of abundance

The abundances of the limpet *C. testudinaria* at the three shore levels varied greatly during sampling. A total of 2402 limpets was obtained in 12 month collections with a mean density for the whole period of study of 11.12 ± 4.51 ind.m^{-2}. It is evident that densities were significantly greater at the high shore level, with a mean of 15.79 ± 7.54 ind.m^{-2}, and at the middle shore level, with a mean of 14.67 ± 13.99 ind.m^{-2}, than at the low shore level, with a mean of 2.90 ± 2.44 ind.m^{-2}.

Temporal variability of densities was also very pronounced. Limpets at the high shore level were particularly abundant during the period between December and June. At the middle shore level, the density did not show the same trend. Significant reductions in density, from 44.33 ind.m^{-2} to 3.00 ind.m^{-2} and 27.00 ind.m^{-2} to 4.17 ind.m^{-2}, occurred from October to December and from April to May, respectively. On the other hand, pronounced increases occurred following the period of reduction in April, July and September (Fig. 3). At the low shore level, the density was generally low. Slight increases were found between the periods of June to September (Fig. 3).

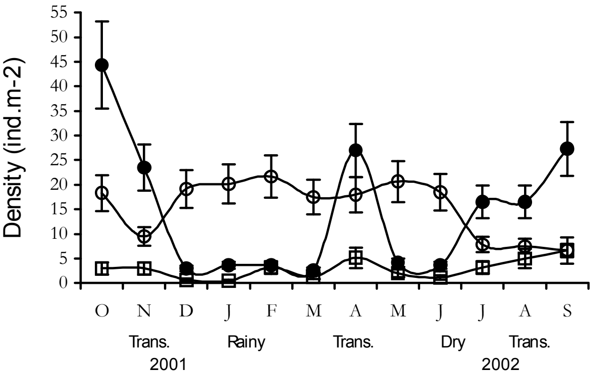
The analysis of variance (ANOVA) of densities of *C. testudinaria* showed significant differences for the shore level, time of sampling, and interaction between shore level and time (Table 3). The percentage of the total sum of squares attributable to the parametric effects in the analysis of variance was 86 %. The effects of the shore level and time of sampling removed 44 % and 16 %, respectively, of the total sum of squares. Orthogonal polynomial was calculated on time of sampling using the total densities pooled from the shore levels, and there were significant interactions between time and shore levels. Thus, three distinct outcomes were evident from the analysis of spatio-temporal variation in abundance. The first involved the variability at small spatial scales, as indicated by the significant differences among the shore levels (Table 3). The next two outcomes consisted of the significant main effect of time and of the interaction between time and shore level. Significant differences in density occurred among the months while preliminary analyses indicated that temporal variation might have confounded estimates of spatial variability between sites sampled at different times (Table 3). A similar pattern was evident by SNK tests, which could discriminate any specific alternative to the null hypothesis in this case. Exactly the same results were obtained by comparing the variances within the time of sampling, indicating that significant change occurred in abundance of limpets throughout the time. Abundance was greater in October and April significantly more often than in March and December.

The dispersion of limpet *C. testudinaria* did not follow any seasonal pattern. In all months, the *MI* values was much greater than 1 (Table 2), implying that the distribution of this species on the three shore levels was highly contagious.

Statistical analysis on the sample dispersions using the Morisita Index (Brower and Zar, 1977) shows a highly significant agreement with the theoretical negative binomial distribution (Table 2), indicating that environmental factors have an effect on the dispersion of the limpets and/or that there was a tendency for individuals to avoid or to move towards each other.

This study shows that the density of *C. testudinaria* was very variable on the three shore levels examined (Fig. 3), with the density of individuals being greatest at the high shore level running down to the lowest one at the low shore level. Similar patterns were also found by Underwood (1975) for *Cellana*, by Sutherland (1970) for *Acmaea scabra*, by Lewis & Bowman (1975) and Thompson (1980) for *Patella vulgata*, and by Creese (1980b) for *Notoacmaea petterdi*. Although Fletcher (1984) reported that population of *Cellana tramoserica* was denser at the mid-shore region than at the high and low intertidal regions of Cape Bank, New South Wales, Australia, and that the abundances of intertidal population were generally higher than those of subtidal populations. In contrast, the abundances of *Patelloida pygmaea* off Wu Kwai Sha, Hong Kong were highest at the lower shore (Liu, 1994), and *Patella flexuosa* occurred only in the lower intertidal zone of the sandstone rocky reef shore near the Seto Marine Biological Laboratory, Japan (Iwasaki, 1998).

Besides the clear spatial pattern, there was also a pronounced seasonal variation. The mean density of *C. testudinaria* was greater at the middle than at high or low shore levels in April and from July to October, while it was greater at the high shore level during rainy season (Fig. 3). This resulted from an increase in abundance at the middle shore level from the rainy to the dry season, while a decrease in abundance at the high shore level occurred from the rainy to the dry season. These patterns can be explained as a seasonal response of the animals to physical stress, indicating that insolation is an important factor in tropical intertidal regions, as reported by Moore (1972). The abundance of *C. testudinaria* at the high shore level is reduced during the dry season because in this season most limpets migrated down to lower levels. Field observations showed that many limpets migrated within the intertidal zone and scattered and regrouped at certain places beneath



Note: o-o High shore level; ●-● Middle shore level; ¡-¡ Low shore level.

Figure 3a. Density (ind.m^{-2}) of limpets of *Cellana testudinaria* living at different shore levels (1SD).

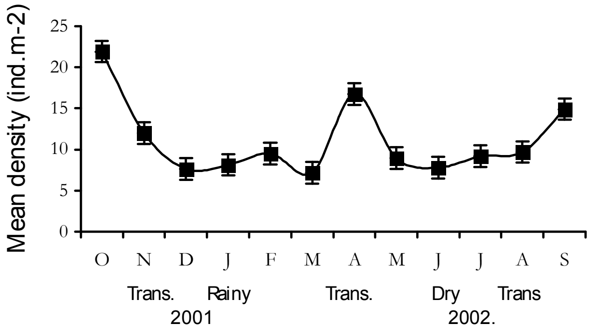


Figure 3b. Mean monthly density (ind.m^{-2}) of limpets of *Cellana testudinaria*, averaged across shore levels.

the boulders at the middle shore level. These movements have been related to temperature changes (Lewis, 1954) of about 40 ^{0}C and are probably regulated by the location of rock pools and crevices on the sheltered side of boulders, which protect the limpets, particularly at low tide, from the heavy insolation. Seasonal migrations have been also observed in *C. testudinaria*, which contributes to the clumped distribution of the limpets. The result of sample dispersion analyses was not surprising and corroborated the findings of many other studies on rocky shores, reporting migration as a prominent process maintaining the spatial structure of assemblages (Liu, 1994).

Higher biomass at the middle shore level in October 2001, April and September 2002 also suggests that limpets migrated to this shore level to avoid desiccation and strong wave action during this month. Small limpets at the middle shore level were proportionally more abundant than large ones in April 2002. By virtue of their smaller size, they can enter shelter from desiccation and wave action. Small-scale migrations occur in many limpet species and have been considered to be a behavioural response to physical stress (reviewed by Branch, 1981; Hartnoll, 1985; Ruiz Sebastián *et al.*, 2002), including avoidance of desiccation (Branch & Cherry, 1985) and survival of wave action (Gray & Hodgson, 1998). Migration patterns can be affected by extrinsic factors including shore height and slope, desiccation and food availability, or by intrinsic factors such as limpet size (Williams *et al.*, 1999; Jenkins & Hartnoll, 2001).

Pattern in assemblages were significantly variable between shore levels. In an analysis of the structure of assemblages on a rock platform in New South Wales (Australia), Underwood (1981) found considerably differences in distribution of organisms from one part of the shore to another and from season to season, in addition to variability among tidal levels. This pattern was related to the effects of spatial physical factors such as slope of the substratum, which is important in maintaining differences between mid-shore and low-shore assemblages (Benedetti-Cecchi, 2001). Therefore, spatio-temporal heterogeneity in the physical features of the habitat could generate spatio-temporal variations in abundance of organisms regardless of the assemblage. This result is consistent with the findings of other studies of rocky shores indicating large differences in the structure of assemblages from top to the bottom of the shore (Southward, 1958; Lewis, 1964), highlighting the importance of physical factors (Benedetti-Cecchi *et al.*, 2000).

Most univariate analyses indicated significant spatial variability and, even more pronounced, temporal variations. These results support a model of spatial distribution of organisms on rocky shores where vertical variability is at least as important as any other scales of variability on an ecosystem (Liu, 1994; Benedetti-Cecchi *et al.*, 1996; Benedetti-Cecchi, 2001). Multivariate analyses produced similar results, which are, however, more complicated in interpretation because of the large number of processes that may potentially regulate the structure of assemblages and the direct and indirect effects of interactions among organisms. This suggests that patterns were primarily governed by biological processes, which is not lost when examining patterns in assemblages (Menge, 1995; Benedetti-Cecchi, 2000). Therefore, the question why these or any other processes contributing to multivariate variation

Table 2. Dispersion indices of *Cellana testudinaria* together with the chi-square test.

Month	N	n	Óx^2	MI	c^2	P
October	394	18	14174	38.09	253.58	< 0.05
November	216	18	4338	21.26	145.37	< 0.05
December	137	18	2479	19.15	188.67	< 0.05
January	146	18	2574	18.66	171.30	< 0.05
February	171	18	3583	22.18	206.03	< 0.05
March	129	18	2203	18.07	178.22	< 0.05
April	301	18	6715	23.62	100.66	< 0.05
May	161	18	3119	20.51	187.88	< 0.05
June	140	18	2326	17.58	158.99	< 0.05
July	165	18	2267	14.54	82.23	< 0.05
August	174	18	2268	13.80	60.58	< 0.05
September	268	18	6360	25.12	196.52	< 0.05

Note: Probabilities that are relevant for interpretation of the results are shown. *N*-total number of individuals; *n*-number of quadrates; *x*-number of individuals per quadrates; *MI*-Morisita Index. c^2-chi square

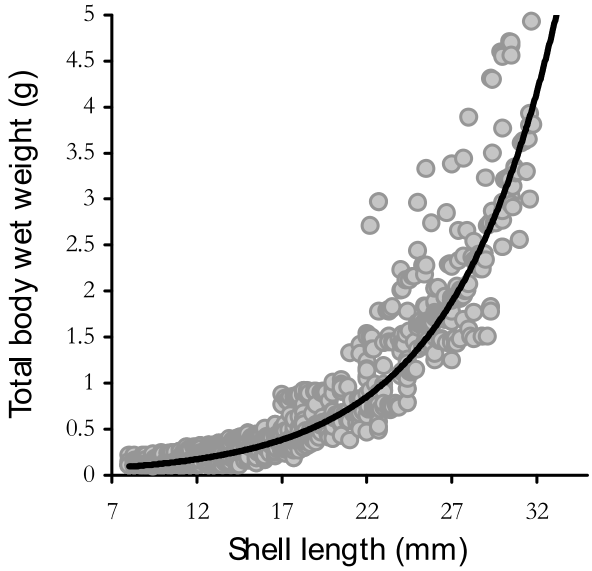


Figure 4. Relationship between shell length (L) and total bodywet weight (W) of *Cellana testudinaria*.

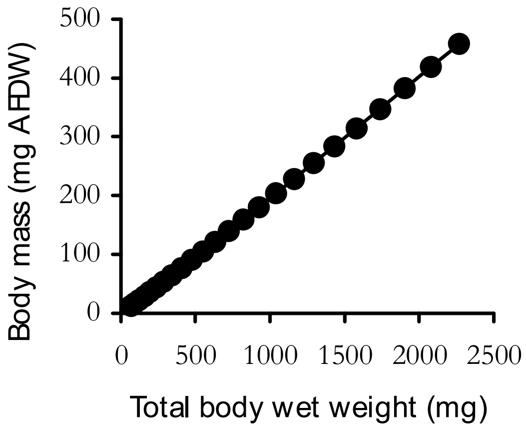


Figure 5. Relationship between total body wet weight (mg) and Body mass (mg AFDW) of *Cellana testudharia*.

produced more variability in distribution and abundance of *C. testudinaria* remain still unknown. Nevertheless, meaningful comparisons of spatio-temporal variation in abundance and biomass were possible. Differences from one level to another within any particular shore, as well inconsistencies in temporal changes, accounted for a proportion of variability in pattern of distribution, which was at least as large as that explained by the differences in environmental gradient.

Length-weight relationships

The 2402 collected specimens ranged in length from 8.0 to 31.8 mm with an average of 16.22 ± 5.26 mm. Their total body wet weight varied between 0.11 and 4.93 g with an average of 0.55 ± 0.70 g. The relationships between shell length and total body wet weight for the whole period of study is given in Table 5 and presented in Figure 4.

The power regression equation of this relationship is $W = 0.0002343\ L^{2.6601}$ (r = 0.92). Statistical analysis of the 95 % confidence intervals on the relationship gives the value of A = ± 0.000031 and b = ± 0.0454 (t-test = 27.27, P < 0.05). The monthly relationships between body mass (AFDW) and shell length calculated from 600 specimens (50 specimens collected in each month) gives an overall relationship of $BM = 0.03236\ L^{2.7703}$ (r = 0.95). The standard deviations (SD) of the intercept-A and the variable-b of this relationship are 0.0178 and 0.3813, respectively.

Conversion factors

The ash-free body weight (mg AFDW) and total body wet weight (mg WW) of mid-size classes, computed using the equations $W = 0.2343\ L^{2.6601}$ and $BM = 0.03236\ L^{2.7703}$ were used to estimate a WW-AFDW conversion factor (Table 6). The linear relationship is $BM_{(mg\ AFDW)} = -5.1361 + 0.2026\ W_{(mg)}$ (Fig. 5), which is highly significant (r = 0.99). Ratios of AFDW/WW range from 0.17 to 0.20 with an average of 0.19 ± 0.0018, indicating that body weight (mg AFDW) of specimens is on average 19 % of the total body wet weight (mg WW). The mean energy content of *C. testudinaria* from Ohoiwait is 21.59 kJ.g^{-1} AFDW.

Biomass

The population biomass values were calculated from the mean density of *C. testudinaria* multiplied by the monthly mean AFDW of specimens (Table 3). The average biomass was 1012.84 ± 748.10 mg AFDW.m^{-2}. A loss in population biomass between October 2001 and January 2002 was followed by an increase, reaching the highest value of 3235.75 mg AFDW.m^{-2} in September 2002 (Fig. 6). The lowest monthly biomass of 544.49 mg AFDW.m^{-2} was recorded in March 2002 (Fig. 6). The monthly mean biomass during the rainy season (619.08 mg AFDW.m^{-2}) was lower than during the dry season (899.01 mg AFDW.m^{-2}).

Variations in monthly mean biomass of *C. testudinaria* at the three different shore levels are summarised in Table 4.

From Figure 7, it can be seen that the biomass of limpets living at the high shore level was higher than at the other shore levels during the rainy season (December-February), whilst during the dry season (June-August), the mean biomass of limpets living at the middle shore level was higher than at the other two shore levels.

Two-way ANOVA shows that biomass differences among shore levels and months were significant (F = 2.49 and 4.61, P < 0.05).

Effects of environmental variables

The distribution and abundance of intertidal limpets are considerably influenced by environmental conditions. Early studies of rocky shores in temperate regions have explored the responses of vertically separated groups of organisms to presumably steep environmental gradients (Sutherland, 1970; Wallace, 1972), which affect the exposure of organisms to the tidal regime (Smith, 1975), and wave action (Stephenson & Stephenson, 1949; Southward, 1958; Lewis, 1964). Several aspects such as height of splash, latitude of locality, timing of low water spring tides, and presence or absence of food were also considered as important factors determining the upper limits of the distribution of the species (Evans, 1947; Southward & Orton, 1954). For instance, the upper limit of *Patella aspera* is reported as the mean high water of neap tides (Southward & Orton, 1954). Off Ohoiwait, immerse and splash to the water during tidal excursion are the critical factor that affects *C. testudinaria* more abundant at the middle shore level on the period between September to November. Unfortunately, it is not evident whether there is any direct physiological necessity for exposure to the wave action or to the water during immersion at some stage in the life of *C. testudinaria*, or whether the effect is an indirect one. Thus, it is important to distinguish between response variations attributable to vertical height on the shore and those attributable to the amount of wave action the shore receives. Nevertheless, the high density in April presumably indicated that wave

Table 7. Monthly mean biomass of *Cellana testudinaria*.

Date	Density ($ind.m^{-2}$)	B M (mg AFDW)	Biomass (mg AFDW.m^{-2})
October	21.89	59.07	1293.07
November	12.00	71.27	855.24
December	7.61	86.46	657.95
January	8.11	68.56	556.00
February	9.50	67.71	643.29
March	7.17	75.94	544.49
April	16.72	58.87	984.25
May	8.94	76.85	687.00
June	7.78	74.50	579.59
July	9.17	88.53	811.80
August	9.67	135.02	1305.64
September	14.89	217.31	3235.75
Mean	11.12	90.00	1012.84

Note: Density is derived from Fig. 3.2 and body mass (BM) from the equation $BM_{(mg\ AFDW)} = 0.2026\ W_{(mg)} - 5.1365$.

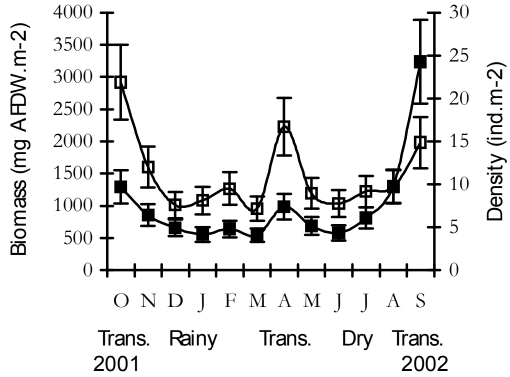


Figure 6. *Cellana testudinaria*. Monthly means of biomass (n) and density (") for all size classes of limpets collected from the three different shore levels. Vertical lines represent standard deviation.

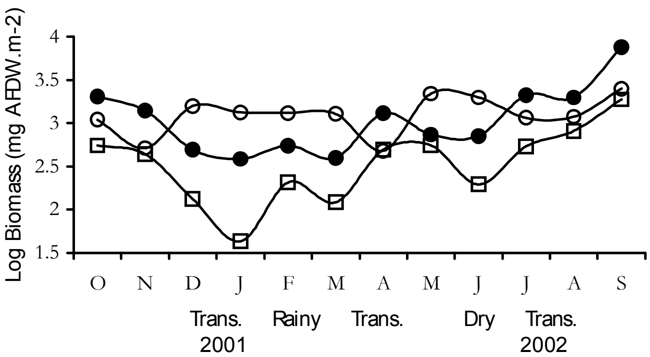
Table 8. Summary of monthly mean biomass of limpet *C. testudinaria* living at the three different shore levels.

Date	High shore			Middle shore			Low shore		
	D	B M	B	D	B M	B	D	B M	B
October	18.33	60.30	1105.36	44.33	45.92	2035.58	3.00	184.50	553.49
November	9.50	54.23	515.14	23.50	59.70	1402.84	3.00	146.00	438.01
December	19.17	82.59	1583.24	3.00	165.66	496.97	0.67	198.48	132.98
January	20.17	66.38	1338.91	3.67	105.28	386.38	0.50	86.03	43.02
February	21.67	60.71	1315.55	3.67	149.85	549.96	3.17	65.37	207.22
March	17.50	73.47	1285.77	2.67	149.04	397.94	1.33	91.71	121.97
April	18.00	26.67	480.09	27.00	48.55	1310.92	5.17	95.35	492.98
May	20.67	106.50	2201.27	4.17	177.41	739.78	2.00	276.68	553.36
June	18.50	107.51	1988.92	3.67	194.42	713.54	1.17	167.88	196.42
July	7.83	147.83	1157.48	16.50	128.17	2114.88	3.17	170.11	539.26
August	7.50	158.77	1190.75	16.50	120.48	1987.85	5.00	163.02	815.11
September	10.67	235.35	2511.18	27.33	278.91	7622.57	6.67	282.35	1883.29

Note: *D*-density ($ind.m^{-2}$); *BM*-body mass (mg AFDW); *B*-biomass (mg AFDW.m^{-2}).

action is an important factor of the precise nature of the effects, because significant numbers of limpets were found at higher shore levels, coinciding with higher wave action. Branch (1981) pointed out that many limpets occur intertidally and are subject to intermittent wetting and drying during each tidal cycle. Several physical factors, therefore, may potentially be stressful under these conditions, including desiccation, temperature and salinity. These factors are often inter-related so that it is often not possible to separate their effects under field conditions. Although the present study did not investigate causal processes explicitly, the patterns described here may provide some clues on the causes of the spatial and temporal variation in the distribution of limpets at the intertidal of Ohoiwait, and were successful in identifying the factors which most probably regulated the spatio-temporal heterogeneity.

The structure of intertidal limpet assemblages cannot be predicted reliably on the basis of vertical position on the shore alone. This study has shown that environmental factors may influence patterns of the distribution of intertidal populations both directly, by imposing physiological constraints on their life, and by mediating their activity. In some cases, physical factors may operate additively. This may occur, for example, during the dry season in the upper shore habitats where the annual variation of the average insolation was highest. Desiccation resistance is one physiological response related to the insolation, which may be variable and allow a species to inhabit a variety of intertidal areas. Previous studies of desiccation response have shown that upper intertidal limpets are able to withstand greater loss of body water than lower intertidal conspecifics (Wallace, 1972; Branch, 1981). The patterns of variation in distribution and abundance documented in the present study can be expected to also occur on other rocky shores of the tropical regions. In conclusion, the results of this study indicated that environmental variables are good predictors of



Note: O–O high shore level; l–l middle shore level; "-" low shore level.

Figure 7. Monthly mean biomass of *C. testudinaria* living at the three different shore levels.

the distribution and abundance of limpets in the intertidal regime, even though it is not feasible to determine the single most important factor.

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