

Intraspecific Variation in Growth Rate among Three Populations of the Intertidal Gastropod, *Nerita japonica* (Dunker)

Variasi Intraspesifik dalam Kecepatan Tumbuh di antara Tiga Populasi Gastropoda Intertidal, *Nerita japonica* (Dunker)

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Abstract

The aim of the present research is to figure out the growth rate of *Nerita japonica* occurring in three different intertidal habitat of Amakusa Shimoshima Island, western Kyushu, Japan. Rocky shore population (R1) and other two stony shore populations (S3u and S3l) were described based on: its mean growth rate, seasonal mean growth rate pattern, the relationship between growth rate and body size. Data recorded in every two months for a year investigation. The results revealed that there were growth rate variations among three snail populations; rocky shore population is faster growth than other two populations (S3u and S3l). Seasonal growth pattern also varied among them. Growth rate peak occur in May–July for R1, and July–September for S3u and S3l. On the other hand, three populations (R1, S3u and S3l) showed the slowest growth rate occur during November–March. Growth rate decreased significantly with increase in initial body size during growth rate period investigated, with the exception of in November–March, only in two out of three populations, growth rate decreased significantly with increase in initial body size. There was a seasonal intraspecific variation in growth rate among three populations of *N. japonica* over even small geographic distances.

Key words: Body size, seasonal growth rate, intraspecific variation, *Nerita japonica*

Abstrak

Untuk mengetahui kecepatan tumbuh *Nerita japonica*, maka diadakan penelitian pada populasi-populasi yang hidup pada tiga macam habitat yang berbeda di Pulau Shimoshima Amakusa, Kyushu bagian barat, Jepang. Parameter yang diamati adalah kecepatan tumbuh rata-rata, pola kecepatan tumbuh rata-rata musiman, dan hubungan antara kecepatan tumbuh dan ukuran tubuh diantara tiga populasi. Pengamatan dilakukan dalam waktu dua bulan selama satu tahun sehingga dapat diketahui variasi menurut musim. Ketiga populasi memperlihatkan kecepatan tumbuh yang berbeda. Populasi pantai *rocky* tumbuh paling pesat dan populasi pantai *stony* bagian atas paling lambat. Pola kecepatan tumbuh ketiga populasi, bervariasi menurut musim. Populasi pantai *rocky* memiliki kecepatan tumbuh maksimal pada periode pertumbuhan Mei–Juli, sedangkan dua populasi pantai *stony* pada Juli–September. Pada bulan November–Maret tahun berikutnya ketiga populasi tumbuh sangat lambat. Kecepatan tumbuh ketiga populasi berkurang secara signifikan seiring bertambahnya ukuran tubuh, kecuali pada November–Maret tahun berikutnya, satu dari tiga populasi tidak memperlihatkan hubungan antara kecepatan tumbuh dan ukuran tubuh. Dapat disimpulkan terdapat variasi intraspesifik pada *N. japonica* dalam hal kecepatan tumbuh menurut musim dan habitat walaupun dengan jarak geografi yang pendek.

Kata kunci: Ukuran tubuh, kecepatan tumbuh musiman, variasi intraspesifik, *Nerita japonica*

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Introduction

The different life history patterns could be found both among and within species,

suggest that organisms should attempt to maximize their fitness (Fisher, 1930). Investigations of intraspecific variations in different habitats are important to understand

life history patterns (Stearns, 1976). It remains to prove whether differences among populations are due to genetic differences among populations, environmental differences among habitats, or a combination of both.

The growth rates of intertidal animals vary with shore height (Paine, 1969; Sutherland, 1970; Underwood, 1984; Jardine, 1985; Takada, 1995), wave action (Hughes, 1972; Janson, 1982; Brown and Quinn, 1988; Etter, 1989), algal food availability (Branch and Branch, 1980; Branch, 1981; Underwood, 1984), and intraspecific competition (Underwood, 1976, 1978; Branch, 1981; Creese and Underwood, 1982). Variation among local subpopulations can be explained by local variation in both biotic and abiotic factors including food abundance, strength of competition, and habitat structures (see reviews in Underwood, 1979; Branch, 1981).

The behavior, age, and growth of *N. japonica* have been firstly observed on rocky shore in Shimoda, Izu, Japan (Suzuki, 1935a, b). Variation in the morphometry of egg capsules and embryos, relationship between fecundity and sizes of capsules and embryos, and relationship between adult body size and reproductive traits of *N. japonica* have been investigated among eight local populations occurring in different intertidal habitats of Amakusa Shimoshima Island, western Kyushu, Japan (Paruntu and Tokeshi, 2003). Intra and inter-specific variation in the morphometry of four intertidal gastropods species, i.e., *Monodonta labio* and *N. japonica* from western Kyushu, Japan, and *N. polita* and *N. exuvia* from Manado, Indonesia have been also investigated by Paruntu (2005). It is assumed, therefore, that individuals of *N. japonica* from different populations may show variation in growth rate, which may in turn be associated with body size. The aim of this study is to determine variation in growth rate among three local populations of *N. japonica* inhabiting different intertidal habitats of Amakusa Shimoshima Island, western Kyushu, Japan. Specifically, we focused on (1) variation in the mean growth rate, (2) variation in the seasonal mean growth rate pattern, and (3) the relationship between growth rate and body size.

Materials and Method

Study Sites

This study was conducted on the Tomioka Peninsula (32°31' N, 130°02' E) of Amakusa Shimoshima Island, south-western Japan (Fig. 1). One study site was established on an exposed intertidal rocky (i.e., the upper Akaiwa rocky shore 1 (R1)) and two study sites on among moderately exposed intertidal stony shore (i.e., two tidal zones of the Magarizaki stony shore 3, the upper stony shore (S3u) and lower stony shore (S3l)) (Fig. 1, Table 1). On the rocky shore 1 (R1), only the upper zone was exclusively used because preliminary observation indicated that *N. japonica* occurred only in this region. The slope of this rocky was steep, whereas that of stony shore was gentle. Shore height difference between the lower (S3l) and upper (S3u) stony shores was 58 cm, that between the lower stony (S3l) and upper rocky (R1) shores was 71 cm, and that between the upper stony (S3u) and upper rocky (R1) shores was 13 cm. There was no significant shore height difference between the upper rocky (R1) and upper stony (S3u) shores. For a general description of these shores, see Mori and Tanaka (1989), Takada and Kikuchi (1990), Paruntu (2003), Paruntu and Tokeshi (2003), and Paruntu (2005).

Maximum Body Size and Density

At least 125 individuals were collected from each of three populations (R1, S3u, and S3l) by using a quadrat in August, 2001. The size of each individual was measured with digital electronic caliper to the nearest 0.01 mm. Large individuals constitute 8% of all in each population (at least 10 large individuals in each population) were used for analysis. Further, densities of the three populations (R1, S3l, and S3u) were estimated by using a quadrat in October, 2001. The data were converted to density per square meter for analysis.

Growth Rate

Mark and recapture experiments were carried out every a two months growth period for one year, i.e., from May–July 2001, July–September 2001, September–November

2001, November 2001–January 2002, January–March 2002, and March–May, 2002, to estimate growth rate of individuals among three populations (R1, S3u, and S3l). A total of about 1897 individuals of the R1, 2432 individuals of the S3l and 2281 individuals of the S3u (these numbers including individuals of the repairing tagged snails of each recaptured time) were collected over the size range (> 4 mm in shell length). After drying the shells, one small waterproof paper tag (2 x 2 mm) with numbers written in China ink were attached with quick-drying epoxy resin. Lengths of the shells of these individuals were measured with a digital electronic caliper to the nearest 0.01 mm and released at the site of collection. Thereafter snails were recapture by hand and forceps at about 8-week intervals for one year. After taking measurements, repairing the tags, all snails were released within 72 h. Additional individuals, particularly small ones which were difficult to recapture, were released in the same manner depending on the overall recapture rate on each sampling occasion. Growth rate was calculated for each individual by using the formula:

$$r = \frac{\ln L_t - \ln L_0}{t}$$

Where r the growth rate, L_0 and L_t are the shell length (mm) at time 0 and t , respectively, and r is the time in days.

Transplant

To determine if growth rate of individuals from different populations were fixed genetically, or by the environment in which the juveniles grew, a number of transplants were done. At least 112 individuals (an average of 185 individuals) of 7–12 mm shell length from each of the two tidal zones of among stony shore (i.e., S3u and S3l) and S3u population were measured, marked, and transplanted to rocky shore (R1) and the lower stony shore (S3l) regions, respectively. A similar set of control individuals were also measured and marked, but replaced in their original locations for a period of three months from May to August, 2002 (within among growth season period). After three months period, individuals were collected and length of their shells re-measured.

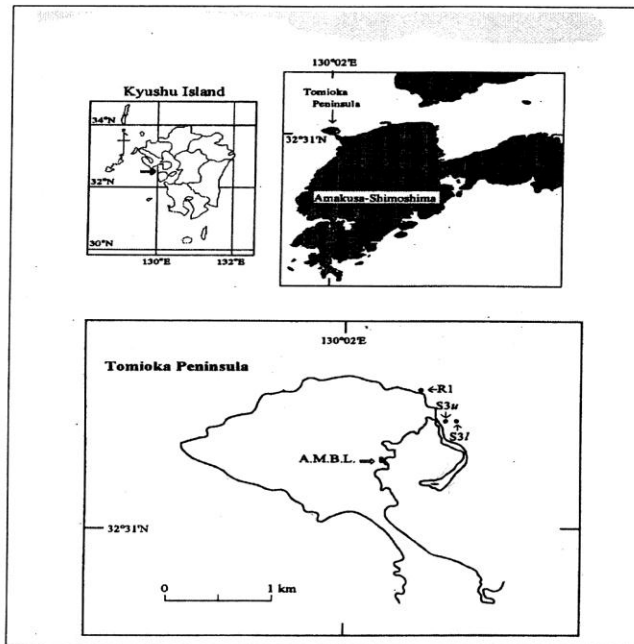


Fig. 1. Map of study area. Location of sampling sites (R1, S3u, and S3l). A.M.B.L.: Amakusa Marine Biological Laboratory, Kyushu University.

Data Analysis

An ANOVA was used to detect whether maximum body size, density and growth rate varied among populations from the three intertidal habitats (Sokal and Rohlf, 1995). If a significant effect was observed, a Tukey-Kramer test for multiple comparisons was used to identify which pairs of sampled differed. Data of growth rates were multiplied by 1000 to stabilize the data. These data of growth rate and initial shell length were then analyzed by regression analysis to examine growth rate-initial shell length relations, and by ANOVA and Tukey-Kramer test to detect difference in growth rate among sites.

Results and Discussion

Maximum Body Size and Density

Maximum body size and density varied considerably among three populations (Tukey-Kramer test, $P < 0.0001$) (Table 1).

Growth rate

Mean growth rate differed significantly among three populations (Fig. 4). The value was larger for the R1 population (1.12), intermediate for S3l population (0.95), and smaller for S3u population (0.61) (Tukey-Kramer test, $P < 0.0001$). Variation in the seasonal mean growth rate of individuals among three populations was shown (Fig. 5). There was a similar cycle of seasonal variability in the rate of growth for two populations (S3u and S3l) at the same geographical location. Mean growth rate of the S3u and S3l populations rose from May until September, 2001 and gradually decline from September, 2001 until March, 2002, then increased again from March to May, 2002. The peak mean growth rate which was achieved by two populations (S3u and S3l) was in July–September, 2001. On the other hand, the peak growth rate that was achieved by the R1 population was in May–July, 2001 and gradually declined from July, 2001 until March, 2002, then increased again from March to May, 2002. During the growth season period investigated, the animals continued to grow from May to November but cease (grow very

slowly) from December to April of the next year. The animals grew faster during the warmer season but in the cold season an arrest of growth (a very slow growth) was shown.

Variation in growth rate of individuals from three populations may in part be a function of variation in the initial body size (shell length) among populations (Fig. 6). Regression analysis revealed that in May–July, 2001 growth season period, in the three populations (R1, S3u and S3l) the growth rate decreased with an increase in initial body size (Fig. 6a). The Tukey-Kramer test revealed that growth rate was larger for the R1 population (2.16) than the S3l and S3u populations (ranging from 0.73–1.05) ($P < 0.0001$); in July–September, 2001, in the three populations (R1, S3u and S3l) the growth rate decreased with an increase in initial body size (Fig. 6b). The Tukey-Kramer test revealed that growth rate was similar for the three populations (R1, S3u and S3l) (1.59–1.80) ($P > 0.05$); in September–November, 2001, in the three populations (R1, S3u and S3l) the growth rate decreased with an increase in initial body size (Fig. 6c), the Tukey-Kramer test revealed that growth rate was larger for the R1 and S3l populations (1.26–1.29) than the S3u population (0.60) ($P < 0.0001$); in November, 2001–January, 2002, in two out of three populations (R1 and S3l) the growth rate decreased with an increase in initial body size (Fig. 6d), while in the S3u population the regression was not significant ($P > 0.05$). The Tukey-Kramer test revealed that growth rate was larger for the S3l population (0.67), intermediate for the R1 population (0.26), and smaller for the S3u population (0.02) ($P < 0.0001$); in January–March, 2002, in two out of three populations (R1 and S3l) the growth rate decreased with an increase in initial body size (Fig. 6e), while in the S3u population the regression was not significant ($P > 0.05$). The Tukey-Kramer test revealed that growth rate was larger for the S3l population (0.37), intermediate for the R1 population (0.22), and smaller for the S3u population (0.08) ($P < 0.0001$); in March–May, 2002, in the three populations (R1, S3u and S3l) the growth rate decreased with an increase in initial body size (Fig. 6f). The Tukey-Kramer test revealed that

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growth rate was larger for the S3l population (1.01) than the R1 and S3u populations (0.36–0.54) ($P < 0.0001$). During this study,

the growth rate of smaller animals was faster than that of the larger and the most vigorous growth was seen from June to October.

Table 1. List of populations (sites) sampled, habitat type, wave exposure, maximum body size in mm (mean \pm 1 S.E.), and density (mean \pm 1 S.E.) per square meter.

Population	Symbol	Habitat Type	Wave Expose	Maximum Body Size (mm)	Density (Individuals/m ²)
Upper stony shore 3, Magarizaki	S3u	stony	intermediate	9.7 \pm 0.10	271 \pm 31.6
Lower stony shore3, Magarizaki	S3l	stony	intermediate	12.8 \pm 0.08	155 \pm 34.4
Upper rocky shore 1, Akaiwa 1	R1	rocky	exposed	15.3 \pm 0.13	3 \pm 1.2

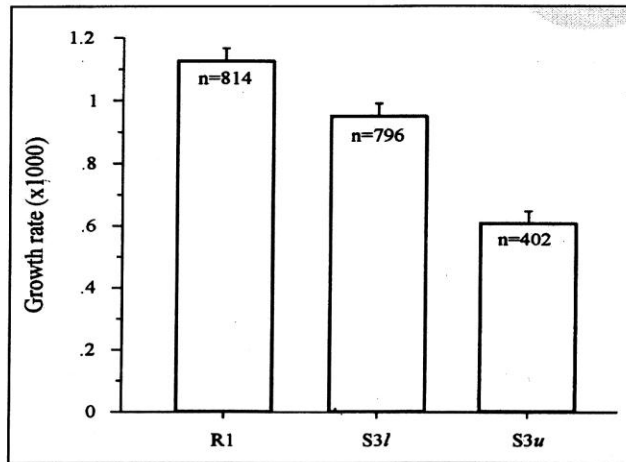


Fig. 4. Mean growth rates (x1000) \pm 1 S.E. of *Nerita japonica* individuals for the three populations (all sampling months for each population combined). *n*, number of the marked individuals examined.

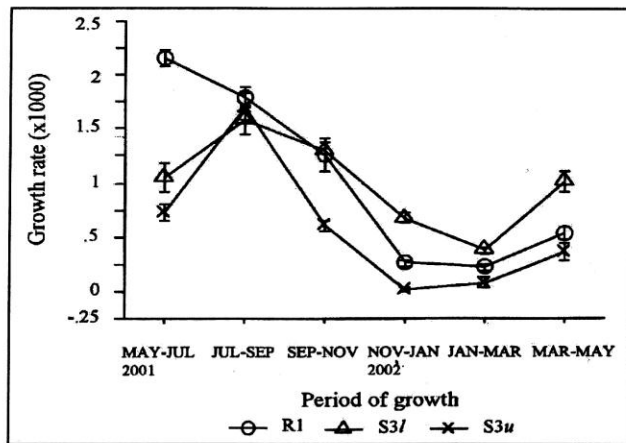


Fig. 5. Mean growth rates (x1000) of *Nerita japonica* individuals estimated in each two months period for one year (*i.e.*, from May–July, 2001 to March–May, 2002) for three populations. Vertical lines indicate \pm 1 S.E. for each population.

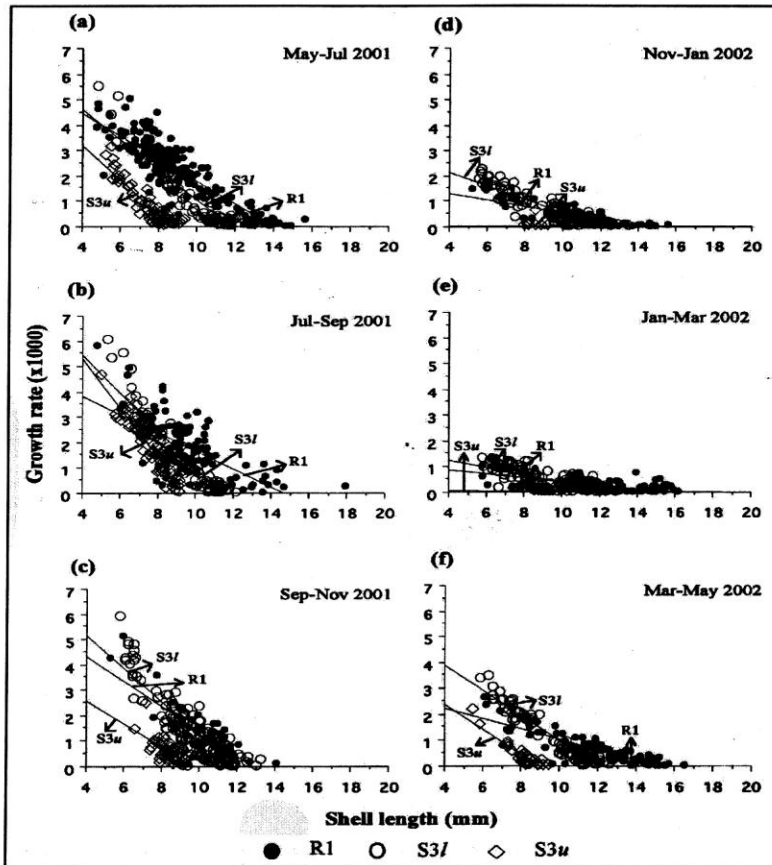


Fig. 6. Comparison among three local populations of *Nerita japonica* (R1, S3l and S3u) of the relationship between growth rates ($\times 1000$) and initial shell length (mm), which was estimated in each two months period for one year (*i.e.*, from May–July, 2001 to March–May, 2002). *n*, number of the marked individuals examined.

Regressions are:

- (a) ● R1: $y = 6.24 - 0.45x$, $n = 233$, $r^2 = 0.75$, $P < 0.0001$
 ○ S3l: $y = 7.03 - 0.60x$, $n = 80$, $r^2 = 0.85$, $P < 0.0001$
 ◇ S3u: $y = 5.97 - 0.69x$, $n = 84$, $r^2 = 0.82$, $P < 0.0001$
- (b) ● R1: $y = 5.31 - 0.36x$, $n = 120$, $r^2 = 0.42$, $P < 0.0001$
 ○ S3l: $y = 8.39 - 0.74x$, $n = 107$, $r^2 = 0.88$, $P < 0.0001$
 ◇ S3u: $y = 9.16 - 0.97x$, $n = 72$, $r^2 = 0.87$, $P < 0.0001$
- (c) ● R1: $y = 6.32 - 0.49x$, $n = 46$, $r^2 = 0.56$, $P < 0.0001$
 ○ S3l: $y = 7.81 - 0.66x$, $n = 186$, $r^2 = 0.79$, $P < 0.0001$
 ◇ S3u: $y = 4.39 - 0.45x$, $n = 63$, $r^2 = 0.56$, $P < 0.0001$
- (d) ● R1: $y = 1.82 - 0.13x$, $n = 120$, $r^2 = 0.68$, $P < 0.0001$
 ○ S3l: $y = 3.24 - 0.27x$, $n = 149$, $r^2 = 0.83$, $P < 0.0001$
 ◇ S3u: $y = 0.02 - 0.002x$, $n = 66$, $r^2 = 0.002$, $P > 0.05$
- (e) ● R1: $y = 1.16 - 0.08x$, $n = 167$, $r^2 = 0.44$, $P < 0.0001$
 ○ S3l: $y = 1.83 - 0.15x$, $n = 177$, $r^2 = 0.59$, $P < 0.0001$
 ◇ S3u: $y = 0.07 - 0.003x$, $n = 78$, $r^2 = 0.001$, $P > 0.05$
- (f) ● R1: $y = 3.06 - 0.20x$, $n = 128$, $r^2 = 0.77$, $P < 0.0001$
 ○ S3l: $y = 5.85 - 0.49x$, $n = 97$, $r^2 = 0.92$, $P < 0.0001$
 ◇ S3u: $y = 4.29 - 0.48x$, $n = 38$, $r^2 = 0.78$, $P < 0.0001$

Transplant

Individuals transplanted from stony shore populations (S3l and S3u) to rocky shore region (R1) and those from the control position (R1), almost all were lost (< 10 individuals of each population were present) when sampling ended, then the data were not used for analysis. However, individuals transplanted from the S3u population to the S3l region, all showed among marked increase in their rate of growth when compared to individuals left in the control position in the S3u area (Tukey-Kramer test, $P < 0.0001$) (Fig. 7). There was also difference between the S3u individuals transplanted to the S3l site and individuals from the control position (S3l) (Tukey-Kramer test, $P < 0.02$).

Three populations of *Nerita japonica* differed markedly in many of the population variables measured during this study (Paruntu, 2003; Paruntu and Tokeshi, 2003; Paruntu, 2005). Maximum body size of snails varied among populations with snails from the S3u population ceasing growth at small size, snails from the S3l population ceasing growth at intermediate size, while snails from the R1 population ceasing growth at large size. Differences in size may be related to a number of factors. Maximum body size of *N. japonica* may be related to density, but be not related to tidal height, indicating that the availability of food may be the limiting factor effecting growth as the density increased.

The very low density of *N. japonica* on an exposed rocky shore compared with a moderately exposed stony shore concur with the pattern increases *Nerita atramentosa*, where densities were very low on an exposed shore compared to those on a sheltered shore (Underwood, 1975b). Underwood (1975b) showed that these differences in density between shores for *N. atramentosa* primarily reflected the effect of exposure to wave action. Predation should be less important on a more exposed rocky shore because exposed shores generally suffer less predation (Menge, 1978a, b, 1983). The relatively low density of *N. japonica* in the lower stony shore compared with the upper stony shore concur with the pattern found in *Neritidae* (*Nerita undata*, *N. scabricosta*, and *N. sanguinolenta*), where

densities were lower in the lower shore relative to those in the upper shore (Vermeij, 1972). Vermeij (1972) showed that predation and other biotic interaction account for much of the mortality at low levels of the shore.

Growth rate of *Nerita japonica* differed among three populations, similar result for *N. atramentosa* that was obtained by Underwood (1984). Differences in growth rate among populations for a number of other grazing gastropods have been investigated by Paine (1969), Sutherland (1970), Lewis and Bowman (1975), Creese (1980), McCormack (1982), Fletcher (1984b), Jardines (1985), and Takada (1995). Differences in growth rate among populations of *N. japonica* in this study reflected differences in maximum body size of individuals from each of the three populations. Thus, the upper R1 population grew the fastest, the lower S3l population grew intermediate, and the upper S3u population grew slowest.

Growth of *N. japonica* may be not related to tidal height, but be related to density of the snail at a site, indicating that the availability of food may be the limiting factor affecting growth as the density increased. Intraspecific competition at increased densities has been found to greatly affect the growth mortality of *N. atramentosa* (Underwood, 1976), and for a number of other species (review in Branch, 1981). Thus, intraspecific competition may be a factor in the slow growth and small size of the upper S3u shore individuals of *N. japonica*. However, intraspecific competition for food because of increased density within a population of *N. japonica* and competition with other species require experimental verification.

There was a possibility that differences in growth of individuals were both genetically and environmentally determined because individuals transplanted from the upper S3u population into the lower S3l region increased their growth rates to exceed that of the lower S3l population. Paine (1969) found that the trochid snail *Tegula funebris* grew faster when at lower than at higher levels of the shore, suggesting that *Tegula* grew slowly at high levels on the shore, but after reaching a certain adult size, moved down-shore and increased their rate of growth in response to increased availability of food at the levels.

increased their rate of growth in response to increased availability of food at the levels. Newell *et al.*, (1971) demonstrated a major compensation in the rate of grazing by *Littorina littorea* at different heights on a shore. Snails at higher levels had a much faster rate of movement of the radula whilst grazing, so that the total number of feeding scrapes during the entire period of submersion was similar to that shown by snails from lower on the shore, even though the latter were submersed for longer. Further, another potential complication is the possibility that the size of the radula of species of intertidal gastropods might vary from one height on the shore to another, and thus affect the rate of feeding, by altering the area covered per scrape (Fretter and Graham, 1962). Thus, the fastest growth rate of *N. japonica* individuals transplanted from the upper S3u population into the lower S3l region appears to be extremely attributed to the environmental condition in which individuals are located and differences in rate of feeding (size of the radulae) of the snail between two tidal zone of a stony shore; this remains to be verified in the future.

Seasonal fluctuations of growth rate of *N. japonica* were not consistent across three populations. The highest growth rate of the R1 population was found in May–July, 2001 growth period. On the other hand, the highest growth rate of the S3l and S3u populations were found in July–September, 2001. The animals from all three populations grow fastest during spawning seasons from April to September (Paruntu, 2003). This contrasts with the pattern of *Nerita atramentosa*, where snails did not grow after reproductive maturity was reached (Underwood, 1975a). Similarly, Seapy (1966) found that the growth of *Acmaea limitula* was greatest during the period when the gonads were expanding. Further, the *N. japonica* snails (especially the younger ones) grow very rapidly during warmer season but in the cold season an arrest of growth (very slow growth) was observed. This is consistent with the result for *N. japonica* that was obtained by Suzuki (1935b).

Conclusion

The present study demonstrates that growth rate of *Nerita japonica* may vary markedly over even small geographic distances. Such variability in the basic traits of a species must have important implications for their life history strategy. Further, the present study suggests that differences in growth of *Nerita japonica* among populations may be due to environmental differences among habitats. Future studies should clarify whether differences among populations are due to genetic differences among populations, environmental differences among habitats, or a combination of both.

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